ALBIAN AND CENOMANIAN (CRETACEOUS) SELACHIAN FAUNAS FROM NORTH EAST ENGLAND

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ABSTRACT. Bulk sampling of the marls and marly limestones of the Hunstanton Formation (Red Chalk) and associated deposits at two sites in north-east England has yielded rich and diverse assemblages of small selachians, largely represented by dissociated teeth. This fauna contains over 35 taxa and is dominated by small to very small nectobenthic forms. A large proportion of these are new, and five new species are described: *Protosqualus pachyrhiza* sp. nov., *Pseudospinax heterodon* sp. nov, *Cretorectolobus gracilis* sp. nov., *Parasymbolus reticularis* sp. nov. and *Pteroscyllium ornatum* sp. nov. *Cretascyliorhinus* gen. nov., is erected for *Scyliorhinus destombesi* Cappetta and related forms. The earliest records of *Squalus* and the Etmopterinae are noted. The fauna is considered a specialist low-nutrient selachian fauna probably confined to the North Sea Basin.

THE fossil remains of selachians (sharks and rays) are present, often abundantly, within many rocks of Upper Palaeozoic to Recent age. Despite this widespread occurrence, published records of selachian fossils have often been biased towards certain stratigraphic intervals. Although selachians from the Upper Cretaceous of northern Europe have been well documented (e.g. Woodward 1912; Delinkevicius 1935; Herman 1977; Cappetta 1980*a*), those of the marine Lower Cretaceous have received less attention. Despite this, studies have revealed diverse Barremian (Biddle and Landemaine 1988), Aptian (Cappetta 1975; Batchelor and Ward 1990) and Albian (Biddle 1993) assemblages. The bulk of published research on the Albian selachian assemblages has been carried out on material from the Gault Clay facies (Cappetta 1977*b*; Biddle 1993; Smart 1995). Other than a few records from the Greensand facies of Britain (e.g. Woodward 1889) and a clastic marginal complex of Texas (Thurmond 1971), faunas from other environments are almost unknown. Studies of European Cretaceous selachians have generally been restricted to the Anglo-Paris Basin, with very few studies of pre-Campanian selachians from the North Sea Basin (e.g. Delinkevicius 1935; Müller and Diedrich 1991).

Sampling of the marls within the Hunstanton Formation (Red Chalk) and associated deposits of Northern England has yielded a high diversity selachian assemblage, containing over 35 species, although some of these are represented by specifically indeterminate material. This is dominated by small nectobenthic taxa, a fauna strikingly different from those described from the Gault Clay (Albian) and Lower Chalk (Cenomanian) of the Anglo-Paris Basin.

GEOLOGICAL SETTING

The Hunstanton Formation or Red Chalk was deposited on the East Midlands Shelf and in the Cleveland Basin (north-east England) during the interval between the Middle Albian and the lower Lower Cenomanian (Mitchell 1995, 1996*a*; Mitchell and Langner 1995). Similar deposits of red marls and chalks were also deposited widely throughout the North Sea region (Lott *et al*. 1985; Hancock 1986). We studied selachian faunas from the Hunstanton Formation at two localities: Speeton (North Yorkshire) in the Cleveland Basin; and South Ferriby (Lincolnshire) on the East Midlands Shelf. We have also studied a small amount of material from Rifle Butts (North Yorkshire)(see Text-fig. 1).

The Cretaceous succession at Speeton is particularly complete with a relatively continuous record from the Berriasian (Ryazanian) to the Turonian. The Albian to Cenomanian interval is represented by the upper part of the Speeton Clay, the Hunstanton Formation and the Ferriby Formation. The Albian portion of the Speeton Clay has previously been described by Ennis (1932) and Wright and Wright (*in* Swinnerton 1955). We have logged much of the upper A Beds (Text-fig. 2). The upper A Beds (about 8 m thick, but not fully exposed) consist of bioturbated grey clays with interbedded reddish marls and a prominent bed of unconsolidated greensand (bed UA4, the Greensand Streak) near the base. Full details will be given elsewhere. The upper A Beds range in age from Lower Albian (*Leymeriella tardefurcatum* Zone) to lower Middle Albian (*Hoplites dentatus* Zone). The Hunstanton Formation at Speeton is represented by a 24 m thick unit of alternating reddish marl and nodular reddish or grey micrites (Mitchell 1995). Internal variations have allowed the establishment of five members within the Formation (Mitchell 1995; Text-figs 2 and 3). It ranges in age from lower Middle Albian (*Hoplites dentatus* Zone) to lower Lower Cenomanian (basal *Mantelliceras mantelli* Zone). The Ferriby Formation at Speeton has been discussed by Jeans (1980) and Mitchell (1996*b*). We consider only the lower part of the Ferriby Formation (the Crowe's Shoot Member, 1.7 metres of hard nodular white and pink chalk with some marl partings: Mitchell 1995), and a single comparative sample from the lower Middle Cenomanian (bed SLC11C of Mitchell 1996*b*). Additionally, we have sampled various levels in the Speeton Clay for comparative material from the Hauterivian to Aptian. Mitchell and Langner (1995) considered that the Hunstanton Formation at Speeton was deposited in deep water close to, or below, storm wave base.

The mid-Cretaceous succession at South Ferriby has been discussed by Mitchell and Langner (1995)(Text-fig. 4). The Lower Albian and lower part of the Middle Albian are represented by the Carstone Formation, 0.6 m of ferruginous sand which lies unconformably on the Jurassic basement; it is largely devoid of macrofossils. The Hunstanton Formation consists of 3.2 m of nodular pink and rarely greenish limestones and marls, which are sandy towards the base and more massive towards the top. Near the top of the formation there is a distinctive omission surface beneath which there is an idiomorphic *Thalassinoides* burrow network (Mitchell and Langner 1995). There is extensive evidence of wave reworking throughout the Hunstanton Formation and Mitchell and Langner (1995) suggest that it was deposited in a shallow water environment, perhaps only a few metres to a few tens of metres water depth.

The Hunstanton Formation at Rifle Butts is very thin (0.6 m) and only the upper part of the Upper Albian is represented (Mitchell 1996*a*). It consists of stromatolitic and sponge-rich micritic limestones that were deposited in a subtidal to intertidal environment (Mitchell and Langner 1995).

MATERIAL AND METHODS

We collected bulk samples from all exposed levels in the Hunstanton Formation at South Ferriby and Speeton that could be sampled for selachian remains (i.e. marls and marly limestones). At South Ferriby all the marls within the Hunstanton Formation were sampled, individual samples being up to 70 kg. At Speeton, samples of 2 to 30 kg were taken from levels ranging from the Speeton Clay upper A Beds (Lower Albian) to the Crowe's Shoot Member of the Ferriby Formation (Cenomanian); this included samples from several horizons in all five members of the Hunstanton Formation at Speeton (Text-figs 2-3). The lower part of the Hunstanton Formation (lower Queen Rocks Member) was very poorly exposed, and consequently little Middle Albian material could be collected; whilst the thin, discontinuous nature of the marls in the Cenomanian (Red Cliff Hole and Crowe's Shoot members) prevented large scale sampling. In total, about 260 kg of material from Ferriby and 350 kg from Speeton was sampled. This produced about 1500 selachian teeth and tooth fragments.

The South Ferriby section is well exposed and easily accessible, but the marls are thin, nodular and commonly sandy. Although much of the material breaks down easily, several wet/dry cycles are often needed to break down the bulk of the material. The section at Speeton requires transport of material some distance along the beach, and, in many cases, considerable processing. The Speeton Clay and marls of the lower part of the Hunstanton

Formation generally break down after one or two wet/dry cycles, but material from the upper part of the section requires several freeze/thaw cycles in the laboratory, frequently with the addition of a saturated solution of sodium sulphate before vigorous manual sieving. Most material was sieved at 125 μm, and the fish material picked from the 355 μm or 250 μm residues. The bulk of the selachian material was recovered from these sub-1mm fractions. Concentration with acid was rarely used, as both the calcitic and vertebrate fauna was required for study.

The preservation of the selachian material is on the whole rather poor. There is a very strong incidence of bioerosion by the hyphate boring *Mycelites*, which preferentially attacks the tooth root (Underwood *et al. in press*). This results in the almost complete destruction of roots in a large proportion (85-95 per cent) of specimens, and the destruction of root surface detail in most of those that remain. Many of the larger teeth, especially those of lamniforms, are also split longitudinally, and at some horizons are present as little more than elongate shards. Much of this breakage and removal of roots occurred prior to burial, as adherent foraminifera are occasionally present attached to the broken edges. This has also been recognised within the Gault Clay facies (Biddle 1993). At some levels, there is some degree of exfoliation of the enameloid, especially in small teeth with a relatively thick enameloid layer. Mechanical abrasion of the teeth is generally insignificant, but occurs within the sandy beds 2 and 3 of the Hunstanton Formation at South Ferriby.

SYSTEMATIC PALAEONTOLOGY

The taxonomic scheme and dental terminology that are used here are largely based on Cappetta (1987). Full synonymies and descriptions are provided only where considered necessary for taxonomic review. Some specifically indeterminate material has been included to give a more complete record of taxonomic diversity. Figured specimens are deposited in Liverpool City Museum (National Museums and Galleries on Merseyside; prefix LIVCM).

Subclass ELASMOBRANCHII Bonaparte 1838
Superorder SQUALOMORPHII Compagno 1973
Order SYNECHODONTIFORMES Duffin and Ward 1993
Family PALAEOSPINACIDAE Regan 1906

Genus SYNECHODUS Woodward 1888*a*

Synechodus dubrisiensis (Mackie, 1863)

Plate 1, figures 1-5

Material. 12 near complete teeth along with about 150 fragmented crowns, LIVCM 1998. 20. A-C.

Horizon and localities. Present in many samples (Text-figs 3-5). Speeton: Speeton Clay (bed A5A: lower Lower Albian) to Ferriby Formation (bed SLC11C: lower Middle Cenomanian). South Ferriby: Hunstanton Formation, (bed 2b: Middle Albian to bed 9: middle Upper Albian). Also present in the Hauterivian and Aptian Speeton Clay.

Description. Teeth strongly heterodont with a gradation from a piercing to crushing morphology in anterior to lateral files. Cusps are well defined in anterior teeth, but in posterolateral teeth may be almost absent and evident only as low domes with a radiating ornament. The main cusp is roughly circular in cross section and somewhat lingually curved in anterior teeth. There are at least two pairs of lateral cusplets, although on no specimens were these strongly defined. Both lingual and labial faces of main cusps and lateral cusplets are ornamented by strong folds, at least some of which extend to the apex or, in the lateral cusplets, the well developed cutting edge. Towards the base these folds typically bifurcate or become anastomosing to form a polygonal ornament. The crown is wide, extending some distance down the labial face to form a prominent overhang. The pseudopolyaulacorhize root is expanded lingually and has large folds which project labially. A small, well preserved tooth referred to this taxon (pl. 1, figs. 3-5; LIVCM 1998. 20. c) has a more flared basal face to the root and lacks the pseudopolyaulacorhize folds typical of the genus. This may represent a parasymphyseal tooth; teeth from the symphyseal region having been noted as having a modified root morphology (Biddle 1993, pl. 5, fig. 1).

Synechodus nitidus Woodward, 1912

Plate 1, figure 6

Material. Two near complete teeth and nine or more incomplete to fragmented crowns, LIVCM 1998. 20. D.

Horizon and localities. Speeton: Hunstanton Formation, Queen Rocks Member, bed QR 2 (Middle Albian) to Crowe's Shoot Member (lower Lower Cenomanian). South Ferriby: Hunstanton Formation, bed 6a (lower Upper Albian)(Text-figs 3-5). Also present in the Aptian Speeton Clay.

Description. The lateral teeth are considerably wider than high. The wide crown carries a rather conical main cusp with three or four mesial and one or two distal cusplets. The principal cusp and lateral cusplets project labially to give a flat occlusal surface in one of the teeth, but are somewhat more erect in the others. The crown strongly overhangs the root labially. Ornament is weak, consisting of a few faint ridges on the labial surface of anterior teeth, which become less evident in more posterior teeth. The cutting edge is weak, and absent in the most posterior tooth seen. The pseudopolyaulacorhize root is flat-based with very strong labial folds and numerous foramina on the lingual face.

Remarks. Although generally poorly preserved, this material compares well with teeth of *S. nitidus* from the Albian (Dalinkevicius 1935) and Cenomanian (Woodward 1912).

Genus PARAORTHACODUS Glückman, 1957

Paraorthacodus recurvus (Trautschold, 1877)

Plate 1, figure 7

Material. One anterolateral tooth lacking lateral cusplets, and several isolated cusps probably referable to this taxon, LIVCM 1998. 20. E.

Horizon and localities. Speeton: Hunstanton Formation, Dulcey Dock Member, bed DD 20; (Text-fig.4), (broken cusps from bed DD 6 (upper Upper Albian) to Red Cliff Hole Member, bed RCH 5c (lower Lower Cenomanian)).

Description. This is one of the largest teeth from the Hunstanton Formation at Speeton, with a height of 5 mm. The relatively high, biconvex main cusp is ornamented with a series of fine, non-bifurcating folds on the lower half of both the labial and lingual faces. This ornament continues onto the lateral cusplets, two of which were originally present on the distal side of the main cusp. The cusps are connected by a very narrow crown, which does not form a labial overhang of the root. The root is broad and flat based with well developed labial folds.

Order HEXANCHIFORMES Compagno 1973

Family HEXANCHIDAE Gray, 1851

Remarks. Although isolated cusps of hexanchid teeth are present in almost all of the Hunstanton Formation samples from South Ferriby and Speeton, complete teeth are uncommon. While most of this fragmentary material appears to belong to the described species of *Notorhynchus*, occasional very robust cusps from the Speeton Beck and Dulcey Dock Members at Speeton suggest that a second species of Albian hexanchiform may also be present.

Genus NOTORHYNCHUS Ayres, 1855

Notorhynchus aptiensis (Pictet, 1865)

Plate 1, figures 8-12

Material. 17 nearly or complete teeth and fragmentary remains of more than 58 others, LIVCM 1998. 20. F-J, LIVCM 1997. 51. H.

Horizon and localities. Speeton: Speeton Clay, bed A4 (lower Lower Albian) to Ferriby Formation (bed SLC11C: lower Middle Cenomanian); Also present in lower units of the Speeton Clay (basal Barremian and Aptian). South Ferriby: Hunstanton Formation (bed 2b: Middle Albian to bed 9: middle Upper Albian)(Text-figs 3-5). Also present in the Hauterivian, Barremian and Aptian of the Speeton Clay.

Description. Teeth were found from both lower and upper jaws, including lower symphyseal and upper parasymphyseal teeth. The anterolateral teeth present range from 1.2 - 11.1 mm crown width, suggesting that teeth from both juvenile and adult individuals are represented. This taxon, as in all hexanchiforms, shows a strong degree of monognathic and dignathic heterodonty (Ward and Thies 1987, Siverson 1997). This is particularly evident as a greater number of cusps in lower teeth than upper teeth. Anterolateral teeth have a principal cusp which is triangular and inclined distally. This is followed by between one and five distal cusps, depending on the position of the tooth in the mouth. These decrease regularly in size from the mesial to most distal cusplet. A very small ?anterolateral tooth, probably from a small individual (pl. 1, fig. 12; LIVCM 1997. 51. H) shows only a single distal cusplet, suggesting an increase in cusplet number with ontogeny as in other hexanchiformes (Ward and Thies 1987). In adult lower teeth, these retain a constant angle to the root, whereas in upper and juvenile teeth, successive cusplets may be at a progressively lower angle. The lower half of the mesial edge of the principal cusp frequently has several serrations or cusplets. These are very variable in form, and may be absent altogether in juvenile teeth and immature upper teeth. In larger lower teeth, these serrations are regular in spacing, but vary in their degree of separation from the mesial edge of the tooth. In smaller lower teeth, the cusplet spacing is less regular, and may fuse to form an irregularly serrated blade. The anaulacorhize root is deep and rather massive, with a faint ridge along the lingual face. There are several foramina of various sizes concentrated along this ridge. Two poorly preserved lower symphyseal teeth are generally similar (pl. 1, fig. 11; LIVCM 1998. 20. J), with two cusps pointed in opposite directions and a distal pair of cusplets forming curved heels giving a 'squaliform' appearance. These differ from the rather larger symphyseal tooth figured by Siverson (1997) in lacking a high central cusp. It is therefore likely that the central cusp of the symphyseal teeth is gained during ontogeny. Upper parasymphyseal teeth are rather different, consisting of a single conical cusp, often showing some degree of torsion, and a globular root.

Remarks. Many Cretaceous hexanchiforms have generally been referred to *Hexanchus microdon* (Agassiz, 1833-1844). It is likely that a number of these records refer to *Notorhynchus aptiensis* (Siverson 1997), which appears to be widely distributed across Europe at levels from the Hauterivian to Cenomanian.

Genus HEXANCHUS Rafinesque 1810

Hexanchus sp. indet.

Plate 2, figure 1

? 1991 *Hexanchus* aff. *microdon* (Agassiz 1843); Müller and Diedrich 1991 Plate 1, fig. 5

Material. Two partial crowns, LIVCM 1998. 20. K.

Horizon and localities. Speeton: Ferriby Formation (bed SLC11C: lower Middle Cenomanian)(Text -fig. 4).

Description. The more complete of these fragmentary teeth shows only three complete and one partial cusp, although the nature of the breakage suggests that this crown is not complete. The mesial cusp in unserrated and rather low, being sharply inclined posteriorly. The successive cusps are similar in form and decrease in height only gradually; the third cusp still being 60 per cent of the height of the mesial.

Remarks. Although specifically indeterminate, these teeth can readily be assigned to *Hexanchus* on gross crown morphology. Although *Hexanchus* has previously been recorded from levels throughout the Jurassic and Cretaceous, *Hexanchus* has not been recognised prior to the Cenomanian; figured pre-Cenomanian specimens belonging to species from a range of Mesozoic genera (Ward and Thies 1987; Cappetta 1990). Frequent records of *Hexanchus* from the Cenomanian (e.g. Woodward 1912; Müller and Diedrich 1991) generally refer to specimens of *Notorhynchus aptiensis* (Siverson 1997), with a single specimen from the German Cenomanian (Müller and Diedrich 1991) possibly being co-specific with these teeth. This is therefore one of the earliest records of *Hexanchus sensu stricto*.

Order SQUALIFORMES Goodrich, 1909
Family SQUALIDAE Bonaparte, 1834

Genus SQUALUS Linnaeus, 1758

Squalus sp.

Plate 2, figures 2-4

Material. Two teeth, one well preserved, LIVCM 1998. 20. L-M.

Horizon and localities. Speeton: Ferriby Formation, Crowe's Shoot Member, 0.43-0.55 m above base (lower Lower Cenomanian); and bed SLC 11C (lower Middle Cenomanian)(Text-fig. 4).

Description. The better preserved tooth (pl.2, figs 3-4; LIVCM 1998. 20. M) is strongly linguo-labially compressed, especially the crown which is rather blade-like. The cusp is relatively narrow and directed posteriorly over a semi-circular distal heel. The crown overhangs the root labially, but is rather excavated along its contact with the root lingually. The labial apron is relatively small, and is parallel-sided for much of its length. The lingual boss is small but projects strongly lingually. The root has a generally flat basal face with a distinct ridge along its lingual margin broken by an infundibulum. There is a wide and deep expansion of the basal face, with prominent lobes on either side of the labial apron. There are numerous small foramina on both lingual and labial faces of the root. In the incomplete tooth (pl.2, fig 2; LIVCM 1998. 20. L), the crown is rather high and short and quite bilaterally symmetrical. The mesial edge is irregular, being convex and faintly denticulate anteriorly with a pronounced notch before the straight leading edge of the relatively erect cusp. The distal heel is large and robust. The labial apron is well developed and parallel sided with a bulbous tip. The root is unknown.

Remarks. Although rather different, there is no evidence to suggest that these two teeth do not belong to the same species, as they show no more variation in morphology than is seen within the heterodonty of the type species of *Squalus*, *S. acathius* Linnaeus 1758. Although abundant and diverse in the Campanian (e.g. Müller and Schöllmann 1989) and Maastrichtian (e.g. Siverson 1993), *Squalus* has not previously been recorded in pre-Campanian rocks; Cenomanian and Turonian squalids (Dalinkevicius 1935) being referable to *Protosqualus* (Cappetta 1987). Although this therefore represents a considerable range extension for *Squalus*, this is not unexpected as other dentally advanced squalids (*Protosqualus*) are known from sediments as early as Barremian (Thies 1981).

Genus PROTOSQUALUS Cappetta, 1977*b*

Protosqualus sigei Cappetta, 1977*b*

Plate 2, figures 5-8

Material. About 460 teeth from all parts on the jaw, ranging from pristine to partial or poorly preserved crowns, LIVCM 1998. 20. N-R.

Horizon and localities. Present in most horizons sampled (Text-figs 2-4). Speeton: Speeton Clay, bed A3C (upper Lower Albian) to Ferriby Formation, bed SLC11C (lower Middle

Cenomanian). South Ferriby: Hunstanton Formation, bed 1 (lower Middle Albian) to bed 9 (middle Upper Albian).

Description. The majority of the teeth correspond well to previous descriptions (Cappetta 1977*b*; Müller and Diedrich 1991; Biddle 1993). The main cusp is relatively narrow and strongly inclined posteriorly with an unserrated mesial edge which is straight or slightly convex for most of its length. Occasional specimens have a notch along the mesial edge of the cusp, but in other respects do not differ from normal anterior teeth. The distal heel is roughly semi-circular and extends slightly posteriorly of the point of the main cusp. The labial apron is well developed and broad, extending below the basal face of the root, but may be narrower and almost parallel-sided in some very small teeth. There is a well developed lingual bulge which is narrow and often rather pointed. The root is low and flat-based and rather expanded lingually with well developed foramina on the labial face. Most specimens show separate basal and lingual axial foramina; only rarely is an infundibulum developed. The basal face of the root is rather variable, often having a wide mesial expansion, and more rarely, a narrow mesial and distal expansion which may extend below the base of the apron. Posterior teeth show extreme antero-distal elongation. The principal cusp length is over twice the maximum height, whilst this length is nearly matched by the distal heel, now a narrow, horizontal blade.

*Remark*s. Although *Protosqualus sigei* is well known from the Albian (Cappetta 1977b; Biddle 1993; Ward pers. comm.) and Cenomanian (Müller and Diedrich 1991), the Hunstanton Formation assemblage appears to be rather more morphologically variable than those previously described. The variations in root morphology probably relate to subtle dignathic, sexual and ontogenetic heterodonty, as recognised in Maastrichtian *Squalus* species (Siverson 1993).

Specimens of *P. sigei* from the Hunstanton Formation appear to be consistently small, not exceeding 2 mm in length. This compares with the type assemblage in which specimens reach 2.4 mm (Cappetta 1977*b*) and comparative specimens from the Lower Gault at Folkestone that reach 3.2 mm (Text-Fig. 6.). This does not appear to be of taxonomic significance; modern squalids may show regional size differences (Siverson 1993), and similar differences have been noted in other Cretaceous selachian taxa such as *Squalicorax* (Siverson 1992).

Protosqualus pachyrhiza sp. nov.

Plate 2, Figures 9-11; Plate 3, Figures 1-2.

Derivation of name. From the generally bulky root.

Holotype. LIVCM 1998. 20. S.

Stratum typicum. South Ferriby: Hunstanton Formation, bed 6a (lower Upper Albian).

Referred material. One well preserved tooth (LIVCM 1998. 20. T) and fragmentary remains of at least ten others.

Horizon and localities. South Ferriby: Hunstanton Formation, beds 3/4, 6a and 6b/7 (lower Upper Albian).

Diagnosis. Squaliform tooth of generally bulky aspect. Cusp short and robust with straight or sigmoidal anterior edge. Distal heel well developed and rounded in profile. Labial apron with gently sloping anterior and posterior edges and rounded tip projecting below root. Lingual bulge poorly defined. Separate lingual axial and basal foramen. Basal face of root flat with rounded lingual edge. Weak basal expansions of root anterior and posterior of labial apron.

Description. On the type specimen, the mesial edge is faintly convex proximally, with a distinct concavity at the base of the erect cusp. In the other specimens, the cusp is less erect, and the mesial edge is either straight or shows only a faint sigmoidal outline. The cusp is short and thick and only weakly distally inclined. The distal heel is large and semi-circular. The labial apron is very wide, over half the width of the tooth, and shallow, with a gently rounded outline. The labial face of the apron is flat or slightly concave and the apron is composed of rather thick enameloid. The crown strongly overhangs the root labially. The labial bulge is poorly defined, and occurs largely as a swelling of the area of the root/crown junction above the axial foramen.This swollen area is as wide as the base of the cusp and has a rounded tip not projecting lingually far beyond the edge of the root. The root is rather bilaterally symmetrical. The basal face is flat, with poorly developed mesial and distal expansions not reaching the base of the apron. The lingual edge of the basal face is either smoothly convex or with a slight depression anterior to the axial foramen. The lingual axial and basal foramina are relatively small, and an infundibulum has not been observed. Other foramina are also small and few in number, being restricted to the upper lingual and labial faces of the root.

Remarks. *Protosqualus pachyrhiza* sp. nov. is rather similar to *Protosqualus sigei*, but is readily recognised by its generally robust stature with the crown being only weakly compressed, the rounded form of the labial apron and the poorly defined lingual bulge. It is only recorded from the lower Upper Albian at South Ferriby, where it co-occurs with relatively uncommon *P. sigei*. It is, however, absent in rocks of the same age at Speeton where *P. sigei* is extremely abundant. It is therefore possible that *P. pachyrhiza* sp. nov. represented a shallower water ecological analogue to *P. sigei*, being restricted to more nutrient-rich shelf settings.

Squalidae genus indet

Plate 3, Figures 3-6

Material. Two teeth, neither perfectly preserved , LIVCM 1998. 20. U-V.

Horizon and localities. Speeton: Hunstanton Formation, Dulcey Dock Member, bed DD 15 and Weather Castle Member, bed WC 2 (upper Upper Albian).

Description. These small teeth, up to 1.2 mm wide, have a mesial edge that is strongly divided into two parts; a relatively straight proximal section at a low angle to the root, followed by a pronounced notch, and a slightly concave leading edge to the erect cusp. The cusp is narrow and oriented with the distal edge vertical relative to the basal face of the root. The distal heel is large and narrow with a rather triangular profile. The labial apron is large and triangular, extending below the root, and tapers to a rounded point from a base rather wider than that of the cusp. A small lingual boss is present below the cusp at the crown-root junction. The basal face of the root is flat with a compressed distal expansion which does not reach the base of the labial apron. The two axial foramina are well developed, and the basal most is particularly large.

Remarks. This taxon is unlike any previously described squalid tooth, and is very characteristic due to the proximal notch and erect cusp. The quantity and quality of material, however, prevents a specific diagnosis. Teeth referable to *P. sigei* occasionally have a mesial notch, but this species is significantly different in both crown and root morphology.

It is possible that the crown morphology demonstrates a transitional stage between homodont squalid teeth and the trifid cusp on the upper teeth of etmopterids.

Genus EOETMOPTERUS Müller and Schöllmann, 1989 ?

Eoetmopterus ?sp.

Plate 3, Figures 7-8

Material. One fairly well preserved lower tooth, LIVCM 1998. 20. W..

Horizon and locality. Speeton: Ferriby Formation, bed SLC 11C (lower Middle Cenomanian).

Description. This tooth, 1.45mm wide, and strongly labio-lingually compressed, is readily distinguished from the other squalids collected. The occlusal edge of the crown is rather *Squalus*-like, with the root being distinctly etmopterid. The cusp is at a low angle to the root and extends almost to the distal edge of the tooth. Initially, the leading edge is strongly convex, but then straight for much of its length. The cusp is narrow with well developed cutting edges, and overhangs a small and low distal heel. The distal edge of the heel is strongly concave in profile. Labially, the basal edge of the crown does not overhang the root, but merges in to it with the loss of enameloid. Anteriorly, the base of the crown is rather excavated, and curves strongly toward the base at the position of a major foramen. There is a well developed labial apron. This is short and rounded, the base of the crown being straight distally with at least three foramina at the boundary. The crown-root junction is straight and strongly excavated lingually, immediately overlying a very strong longitudinal ridge. This is shallow and basally forms the basal face of the root. There are a number of well developed foramina on both its upper and lower surfaces. The labial face of the root has a deep basal expansion with a distinct anterior notch. This is shallower than in most etmopterids, with no sign of a groove on the lingual face.

Remarks. This taxon seems to represent the earliest specimen of an etmopterid, extending the origins of this group from the Campanian to the Cenomanian. It strongly resembles a Campanian tooth referred to as *Eoetmopterus supracretaceus* Müller and Schöllmann 1989, pl. 4, fig. 3, although this specimen does not appear to belong to the same species as the Type specimen (pl. 4, fig. 4.), with *Eoetmopterus supracretaceus* being based on heterogeneous assemblage of several taxa (Siverson 1993). It is therefore likely that this tooth represents the second record of an unnamed genus with a range from Cenomanian to Campanian, but more material is needed to verify this.

Family ECHINORHINIDAE Gill, 1862 ?

Echinorhinid ? gen. et sp. indet.

Plate 3, Figure 9

Material. Two poorly preserved partial teeth, LIVCM 1998. 20. X.

Horizon and localities. Speeton: Hunstanton Formation, Dulcey Dock Member, bed 16 (upper Upper Albian). South Ferriby: Hunstanton Formation, bed 6b/7 (lower Upper Albian).

Description. The crown is compressed and rather blade-like. The mesial edge is strongly concave leading to a vertical cusp, short on one specimen, rather high on the other, the distal edge of which is weakly convex. The distal heel is wide on the specimen where it is preserved. The labial face is almost flat, and the bioeroded basal edge shows no sign of the former presence of an apron.

Remarks. Despite their very poor preservation, these specimens are sufficient to indicate the presence of another squalid taxon. The affinities are uncertain, but the straight crown base suggests this may represent a member of the Echinorhinidae (e.g. Cappetta 1987).

Superorder SQUATINOMORPHII Compagno, 1973
Family SQUATINIDAE Bonaparte, 1838

Genus SQUATINA Duméril, 1806

Remarks. The tooth morphology of the genus *Squatina* is both simple and conservative. it is therefore unlikely that teeth alone are always going to be a reliable guide to taxonomic identity (Herman 1977; Batchelor and Ward 1990). As a result, many Cretaceous specimens have been referred either to *S. cranei* Woodward, 1888*b* (which is known from a partial skeleton), or *S. decipiens* Dalinkevicius, 1935, depending on whether the teeth are robust or gracile respectively. This situation has further been complicated by the assignment of robust teeth to *S. decipiens* and gracile teeth to *S. cranei* by Cappetta (1975) (Batchelor and Ward 1990), and Biddle (1993). This taxonomic lumping of morphotypes probably conceals the true specific composition of the genus, which would probably only be revealed by detailed study of large populations of teeth, preferably with associated dentitions or skeletons. It is also likely that a large number of Cretaceous teeth figured as *Squatina* are from orectolobiformes such as *Cederstroemia* (Siverson 1995) or related taxa.

Squatina cf. *cranei* Woodward, 1888*b*

Plate 4, Figures 1-2.

1977 *Squatina cranei* Woodward; Herman, p. 123, pl. 5, fig. 2.

Material. About 165 fragmentary teeth and isolated cusps form many of the horizons sampled as well as a single well preserved tooth from Middle Cenomanian, LIVCM 1998. 20. Y.

Horizon and localities. Speeton: Speeton Clay, bed A1B (upper Lower Albian) to Ferriby Chalk Formation, bed SLC 11C (lower Middle Cenomanian). South Ferriby: Hunstanton Formation, bed 2b (Middle Albian) to bed 9 (middle Upper Albian).

Description. The general tooth morphology is relatively heterodont and strongly reminiscent of the extant *Squatina squatina* (Linnaeus, 1758). The teeth have a single cusp which is relatively elongate but still robust and may be either straight or slightly lingually curved. The lateral blades are narrow and taper in some teeth, with a cutting edge running the width of the crown. The labial bulge is triangular or rounded and, at its origin, usually as wide as the base of the cusp. It extends below the base of the root, but does not project labially; the profile of the labial face being straight or slightly convex. The root is relatively narrow and low, being at least twice as wide as the height of the cusp. Lingually, the root is narrow with a well developed enameloid-covered lingual boss. There are a number of small foramina along the upper lingual surface of the root, with a large foramen at the termination of the lingual projection. The basal face is flat with a large basal foramen.

Squatina sp.

Plate 4, Figures 3-4

1975 *Squatina cranei* Woodward; Cappetta, fig. 8.
1993 *Squatina cranei* Woodward; Biddle, p. 199, pl. 1, fig. 2.

Material. At least 15 poorly to well preserved teeth, LIVCM 1998. 20. Z.

Horizon and localities. Speeton: Speeton Clay, bed A4 (lower Lower Albian) to Ferriby Chalk Formation, bed SLC 11C (lower Middle Cenomanian). South Ferriby: Hunstanton Formation, beds 3, 5b and 6a (lower Upper Albian).

Description. The teeth are small (rarely over 1mm high) and gracile in respect to both the crown and root. The cusp is slender and biconvex with a well developed cutting edge that grades into the narrow lateral blades with a smooth but tight curve. There is a slight lingual and occasionally distal curvature. The labial bulge is variable in form, but may project both labially and below the base of the root. The root is roughly diamond shaped in basal view, being relatively expanded lingually for its width. It is low and may be slightly excavated basally. The lingual boss is wide, but relatively low. Foramina are well marked on the upper lingual surface and at the end of the lingual boss.

Remarks. Teeth of this morphology have been figured by Cappetta (1975) and Biddle (1993) as *S. cranei*, probably due to Woodward's (1912) comments on the gracile nature of some *S. cranei* teeth. In general form, however, the Red Chalk teeth resemble far more closely those of *S. decipiens* Dalinkevicius, 1935, although both this species and the (?conspecific) *Squatina* species B of Batchelor and Ward (1990), differ in having a robust labial bulge and overall are larger in size. It is therefore uncertain whether this taxon represents a small form of *S. decipiens* or a separate species.

Superorder GALEOMORPHII Compagno, 1973
Order HETERODONTIFORMES Berg, 1940
Family HETERODONTIDAE Gray, 1851

Genus HETERODONTUS de Blainville, 1816

Heterodontus canaliculatus (Egerton *in* Dixon, 1850) ?

Plate 4, Figures 5-8

Material. One near complete, but abraded, lateral tooth; one well preserved small anterolateral tooth; and one anterior crown. Eight partial lateral crowns are also tentatively assigned to this taxon, LIVCM 1998. 20. AA-AC.

Horizon and localities. South Ferriby: Hunstanton Formation, beds 2 and 5b (Middle and lower Upper Albian) (fragmentary material from South Ferriby: Hunstanton Formation beds 4 to 9 and Speeton: Hunstanton Formation, Weather Castle Member, bed WC 2 (upper Upper Albian) and Ferriby Chalk Formation, bed SLC11C (lower Middle Cenomanian)).

Description. On the lateral tooth (LIVCM XXXX), the occlusal face of the crown is somewhat sigmoidal in outline, tapering to a rounded end. There is a very strong occlusal ridge, rising to an elevated central cusp and smaller lateral cusp. The ornament is somewhat abraded, but with weak transverse ridges visible, whilst strong, rather irregular ridges are seen on the referred partial lateral teeth. The root is massive and overhung by the crown, with a well developed central foramen. The antero-lateral tooth (LIVCM XXXX) is similar, but smaller, and not sigmoidal. It lacks occlusal or labial ornament and has a small erect cusp with a well developed cutting edge. The single anterior tooth (LIVCM XXXX) is triangular in outline and unornamented, with a concave edge to the labial apron and a pair of lateral cusplets reduced to shoulders.

Remarks. The relatively high crown, sigmoidal outline and dominant transverse ornament of lateral teeth correspond well to the specimens of *H. canaliculatus* figured in Woodward (1912) and *H.* cf. *canaliculatus* in Cappetta (1975), whilst the anterior tooth resembles that referred to the third file of *H. canaliculatus* by Herman (1977). *Heterodontus upnikensis* Dalinkevicius, 1935 was erected on anterior teeth lacking lateral cusps, similar to the anterior tooth described here. This name was also used for unornamented small anterolateral teeth by Biddle (1993). Although it is possible that *H. upnikensis* represents a separate taxon, it is more likely that it refers to unornamented (Dalinkevicius 1935) and juvenile (Biddle 1993) teeth of *H. canaliculatus*.

Order ORECTOLOBIFORMES Applegate, 1972

Family HEMISCYLLIIDAE Gill, 1862

Genus CHILOSCYLLIUM Müller and Henle, 1838-1841

Chiloscyllium cf. *greeni* (Cappetta, 1973)

Plate 4, Figure 9

1990 *Chiloscyllium* sp.: Batchelor and Ward, pl. 3, fig. 1a-c.

Material. Five imperfect teeth, LIVCM 1998. 20. AD.

Horizon and localities. Speeton: Speeton Clay Formation bed A1A (lower Middle Albian) and Hunstanton Formation, Weather Castle Member, bed WC 2 (upper Upper Albian). Also recorded in the Lower Aptian of the Speeton Clay.

Description. The teeth are bilaterally symmetrical. The principal cusp is rather elongate and triangular in shape with a well developed cutting edge. The lateral cusplets are poorly developed and present a laterally expanded heel, labial to which is a concavity on the apron profile. The crown is unornamented and only slightly convex. An incomplete root is preserved in one specimen. The root is gracile and narrow, with a relatively low profile. The basal face is strongly 'V'-shaped with a well developed central foramen.

Genus cf. HEMISCYLLIUM Smith, 1837

cf. *Hemiscyllium* sp.

Plate 4, Figures 10-12; Plate 5, Figures 1-2

Material. Seven incomplete teeth, LIVCM 1998. 20. AE-AH.

Horizon and localities. Speeton: Hunstanton Formation, Speeton Beck Member, bed SB 1 (lower Upper Albian). South Ferriby: Hunstanton Formation, beds 5b and 6a (lower Upper Albian).

Description. The teeth represent anterior (including possibly symphyseal) and lateral positions within a relatively heterodont jaw. The crown is only faintly convex and has a large, unornamented labial apron, semicircular in the lateral tooth (LIVCM 1998. 20. AE), but rather more labially expanded anteriorly. On one specimen (LIVCM 1998. 20. AF) it has a slightly concave labial edge. The lingual edge has a triangular principal cusp, rather elongate in the anterior teeth, with one or generally two pairs of lateral cusplets. Where two pairs are present, the inner pair is well developed, but far shorter than the principal cusp, the outer pair little more than lateral heels. There is a narrow cutting edge along the lingual edge of the crown and a poorly developed lingual boss below the principal cusp. Fragmentary material suggests that the root is hemiaulacorhize with a rather high, rounded lingual edge. One anterior tooth is symmetrical, whilst there is some degree of asymmetry within the other teeth. One of the teeth (LIVCM 1998. 20. AG) has only a single pair of lateral cusps and a greater degree of asymmetry than the others. It is unclear, due to the small quantity of material available, whether this is a morphology within the normal range of heterodonty or represents a separate taxon.

Remarks. The overall morphology of the teeth of this species is similar to that of *Hemiscyllium* Smith 1837, but differs from modern forms by the presence of well developed lateral cusplets and a well developed cutting edge. These teeth may therefore represent an as yet unnamed genus of orectolobid closely related to *Hemiscyllium*. Several teeth of very similar morphology have been noted from Lower Cretaceous (Aptian) sediments, and have been referred to the genera *Mesiteia* (Cappetta 1975) and *Heterodontus* (Thies 1979). These are probably congeneric with the taxon described here, and may represent examples of the same species, although the small quantity of material prevents definite synonymy.

Genus PSEUDOSPINAX Müller and Diedrich 1991

Type species. *Pseudospinax pusillus* Müller and Diedrich 1991.

Amended diagnosis. Heterodonty gradient monognathic and, in some species, dignathic or sexual. Labial face flat to slightly convex and oval in outline, being somewhat extended antero-distally. Small principal cusp triangular or reduced and rounded in some lateral teeth. This takes up less than half the width of the occlusal edge, which bears a distinct cutting margin. Lateral cusplets small and triangular, as poorly defined serrations, or absent and do not extend to the lateral edges of the crown. Lingual bulge well developed, especially in lateral files, and enameloid covered almost to base of the root. The hemiaulacorhize root is low and narrower than the crown.

Comparison. The tooth morphology of *Pseudospinax* is superficially rather similar to that of the anterior teeth of some species of *Protospinax* such as *P. annectans* Woodward, 1918 and *P. lochensteinensis* Thies, 1983, but may be distinguished by the lack of a concave labial surface, a lower root with more prominent lingual bulge and a less well defined uvula. The general tooth morphology appears simpler than that of other genera of Hemiscylliids, but appears closer to members of this family than that of other extant groups. It is possible, however, that Mesozoic orectolobids represent a suite of families whose dentition is only superficially similar to modern forms (Cappetta 1987).

It is likely that *Pseudospinax* contains a number of species referred to the genera *Hemiscyllium* or *Protospinax*. Species probably referable to this genus include *Protospinax*? *muftius* Thies, 1983 from Callovian clays of Southern England, *Hemiscyllium hermani* Müller, 1989 from Campanian chalks of Germany and *Hemiscyllium* sp. of Herman 1982 from German Maastrichtian chalks. The referral of these additional taxa to *Pseudospinax* gives the genus a greatly increased range from Callovian to Maastrichtian.

Pseudospinax heterodon sp. nov.

Plate 5, Figures 3-10

Derivation of name. In reference to the wide range of tooth morphologies compared to other members of the genus.

Holotype.LIVCM 1998. 20. AL.

Stratum typicum. Speeton: Hunstanton Formation, Dulcey Dock Member, bed DD 6 (upper Upper Albian)

Referred material. Two complete teeth and nine incomplete teeth and crowns, LIVCM 1998. 20. AJ-AK, LIVCM 1998. 20. AM-AP.

Horizon and localities. Speeton: Hunstanton Formation, Speeton Member, bed SB3 (lower Upper Albian) to Red Cliff Hole Member, bed RCH 5e (lower Lower Cenomanian). South Ferriby: Hunstanton Formation, bed 6a (lower Upper Albian).

Diagnosis. Very small teeth with labial face almost flat. Form of cusps and outline of crown variable due to monognathic and dignathic/sexual heterodonty. Principal cusp is small and narrow, not exceeding length of labial face of crown and almost absent in some lateral files. Lateral cusplets small, not exceeding a quarter of the length of the main cusp and often present as little more than serrations. Uvula wide, but poorly defined over a root far narrower than the crown.

Description. These small (under 1mm in width) teeth show a variation in crown shape that suggests both a graded monognathic heterodonty and a dignathic or possibly sexual heterodonty. The labial face of the crown varies from almost circular to strongly laterally expanded with the width being over twice the height. The surface is flat, with no ornament and only a very slight convexity at the margins. The teeth can be divided into strongly and weakly cuspate forms, both of which show the same range of labial face morphologies. The weakly cuspate teeth have a single triangular cusp directed slightly distally. This is as wide at the base as long, and forms up to one third of the height of the crown. The remaining occlusal edge of the crown has a cutting edge and is smoothly convex in profile. In the more strongly cuspate teeth, the principle cusp is longer than wide, with a well developed cutting edge. It is flanked by a pair of small lateral cusps which are usually rounded in profile. The lingual face of the crown is short and angled acutely to the occlusal edge. The root is hemiaulacorhize, rather low, and displaced strongly lingually. The lingual boss is prominent and has a thin enameloid covering. The lateral and basal foramina are large, but poorly visible in the specimens.

Remarks. The presence of strongly and weakly cuspate specimens with the same range of crown shapes suggests that the presence of elongate cusps is either a dignathic or possibly sexual feature, with both morphologies present in anterior and lateral files. This has not been recognised in other members of this genus, or other Mesozoic orectolobids.

Family INCERTAE SEDIS

Genus ORECTOLOBOIDES Cappetta, 1977b

Orectoloboides parvulus (Dalinkevicius, 1935)?

Plate 6, Figure 1

Material. One lateral and two anterior teeth, all broken, LIVCM 1998. 20. AQ.

Horizon and localities. Speeton: Speeton Clay, beds A4 and A5a (lower Lower Albian).

Description. All teeth are poorly preserved. As in material previously described from the Gault Clay (Albian)(Cappetta 1977; Biddle 1993), the teeth have a slender principal cusp with up to two lateral cusplets in anterior teeth. The labial face of the crown has a small number of irregular longitudinal ridges which may connect with the occlusal edge in lateral teeth.

Genus CRETASCYLLIUM Müller and Diedrich, 1991

Cretascyllium sp.

Plate 6, Figures 2-4

Material. One imperfect tooth, LIVCM 1998. 20. AR.

Horizon and localities. Speeton: Hunstanton Formation, Speeton Beck Member bed SB12 (lower Upper Albian).

Description. The single tooth, 4.2 mm high, has a strongly triangular outline. The cusp is biconvex and relatively compressed linguo-labially and inclined lingually. It is fairly elongate, almost twice as high as wide, and only slightly concave edged. The curve of the edges of the cusp is continued along narrow and poorly developed lateral blades which project weakly labially and basally. The labial bulge is not well developed, being both narrow and compressed, and does not reach the base of the root. The hemiaulacorhize root is rather high and is not expanded lingually. There is no clearly differentiated lingual boss above a raised area toward the lingual apex of the root. The basal face of the root is very strongly excavated, with large foramen on the basal face and lingual apex. There are numerous small foramina around the edge of the basal face.

Remarks. This tooth most strongly resembles *Cretascyllium expansum* Müller and Diedrich 1991 from chalks of the German Cenomanian, but differs from it in having greatly reduced lateral blades, a straighter crown edge and a more gracile root.

Genus CRETORECTOLOBUS Case, 1978

Cretorectolobus gracilis sp. nov.

Plate 6, Figures 5-9

Derivation of name. In reference to the gracile and narrow form of the tooth.

Holotype. LIVCM 1998. 20. AS.

Stratum typicum. South Ferriby, Hunstanton Formation Bed 6a (lower Upper Albian).

Referred material. Three moderately well preserved and at least three partial teeth, LIVCM 1998. 20. AT-AU.

Horizon and localities. Speeton: Speeton Clay, bed A1B (upper Lower Albian) to Hunstanton Formation, Speeton Beck Member, bed SB 6 (lower Upper Albian).

Diagnosis. Small teeth with a single elongate cusp. Cusp narrow and only slightly compressed, with lingual curvature basally. Weak cutting edges continue over tooth to the ends of the lateral blades. Lateral blades short, reaching lateral edges of root with incipient cusplets at extremities. Labial bulge small and rounded, reaching to base of root. Crown overhangs root labially. No well developed lingual protuberance, enameloid not reaching lingual edge of root. Root low and hemiaulacorhize and triangular basally. Basal face deeply excavated, and basal and lingual foramina large. Linguo-dorsal foramina well developed.

Description. The teeth are generally small (up to 3.2 mm high) and show a moderate heterodonty, with narrower anterior and wider lateral teeth. The cusps are bent lingually, but in no teeth are observed to bend distally to any degree. The unornamented cusp is triangular in labial view, only slightly compressed and with a small but continuously developed cutting edge. The labial boss is moderately developed, being rounded and inclined basally, giving the profile of the labial edge a rather pronounced curvature. The lateral blades are short and continue almost to the edge of the root. The ends of the lateral blades are bulbous in some specimens, giving the appearance of an incipient lateral cusplet. There is no true lingual protuberance. The root is thick, triangular in basal view and rather low lingually. The basal face is strongly excavated and a pair of large foramina is present on the basal face and at the lingual apex. There are a number of margino-lingual foramina as well as several on the basal face.

Remarks. In a review of Cretaceous 'squatiniform' orectolobids, Siverson (1995) recognised Cretorectolobus *olsoni* Case 1978 as the only species of *Cretorectolobus*, other similar taxa being referable to *Cederstroemia* Siverson, 1995. *Cretorectolobus gracilis* sp. nov. is very similar in general morphology with *C. olsoni* , but differs in being generally more narrow with less well developed lateral blades, resulting in a more piercing morphotype than the cutting/piercing form of the type species (Siverson 1995). The presence of *Cretorectolobus* in sediments of Albian age represents a far earlier occurrence than the Campanian age of the type species. It is possible that some early Lower Cretaceous (e.g. Thies 1979) and Upper Jurassic (e.g. Thies 1983) teeth assigned to *Squatina* may be referable to *Cretorectolobus,* greatly extending geological range of the genus.

Family PARASCYLLIIDAE Gill, 1862

Genus PARARHINCODON Herman *in* Cappetta, 1976

Pararhincodon cf. *lehmani* Cappetta, 1980*a*

Plate 7, Figures 1-5

Material. Four moderately to well preserved teeth, LIVCM 1998. 20. AV-AX.

Horizon and localities. Speeton: Hunstanton Formation, Weather Castle Member, beds WC 1 and WC 5 (upper Upper Albian). South Ferriby: Hunstanton Formation, bed 6a (lower Upper Albian).

Description. The anterior tooth is very small and antero-distally compressed. The single cusp is bent lingually, its labial face being almost flat and separated from the strongly convex lingual face by a cutting edge which dies out near the tip of the cusp. The low root is hemiaulacorhize with poorly developed lobes. There is a pair of very prominent lateral foramina. The lateral teeth are rather more massive, the cusp being biconvex and rather wide at the base. The cusp is twisted distally and has a small shoulder at its base on the proximal side. The base of the crown is rather bulbous, with an ornament of fine to very fine irregular ridges. This overhangs a constriction at the contact with the low root. The root is bifid, but with a reduced anterior lobe. The lateral foramina are very prominent.

Remarks. The gracile nature of these teeth and the strong overhang of the crown suggest a closer affinity to *Pararhincodon lehmani* Cappeta, 1980*a* from the Cenomanian of Lebanon than to *P. crouchardi* Herman, 1977 from the top Cenomanian and Turonian of Belgium. The degree of heterodonty of *P. lehmani*, however, appears to be rather less than in this material, and so it is possible that a new species is represented. These specimens represent the oldest known occurrence of *Pararhincodon*. There is some doubt as to whether the Cretaceous and Tertiary species referred to *Pararhincodon* belong within the same genus (Ward pres. comm.), and it is therefore possible that the Cretaceous species may be assignable to a new genus.

Order LAMNIFORMES Berg, 1958

Remarks. Although often very common, lamniform teeth tend to be poorly preserved compared with other taxa. They generally lack a root and are frequently split longitudinally. It is therefore likely that although lamniforms were as diverse a part of the assemblage as in the Cretaceous elsewhere (e.g. Biddle 1993), the diversity recorded from the Hunstanton Formation is restricted by the number of identifiable specimens. Most of these better specimens were collected by surface collection from the upper parts of the Speeton section, and, consequently, any species present prior to the terminal Albian are unlikely to be represented. Although several taxa could be identified from this material, the state of preservation makes it unlikely that any new information will be gained regarding the species concerned.

Family MITSUKURINIDAE Jordan, 1898

Remarks. Due to the homeomorphic nature of lamniform teeth, it is possible that a large proportion of the Cretaceous tooth taxa conventially placed within the Mitsukurinidae belong to members of the Odontaspididae or Carcharinidae.

Genus ANOMOTODON Arambourg, 1952

Anomotodon principalis Biddle, 1993, *non* Cappetta, 1975

Text-Figure 6, A-B.

1993 *Anomotodon principalis* Cappetta 1975; Biddle, p. 204, pl. 3, figs. 5-8.

Material. One broken anterior tooth and two crowns, LIVCM 1998. 20. BS.

Horizon and localities. Speeton: Hunstanton Formation, Weather Castle Member, beds WC 1 and WC 6 (upper Upper Albian).

Description. The crown is high and narrow, being rather linguo-labially compressed distally and showing a slight sigmoidal curvature. Ornament is very poorly developed, with about three pairs of faint, somewhat flexuous folds near the edges of the lingual face. There are no lateral cusplets and no significant crown tongue of enameloid extending along the top of the root. The preserved root branch is rather short and bulbous, with a well developed lingual protuberance.

Remarks. Although the tooth is rather similar to specimens from the Gault Clay (Lower to Middle Albian) referred to *Anomotodon principalis* Cappetta, 1975, by Biddle (1993), both this specimen and the material figured by Biddle differ from the type material of *A. principalis* by the lack of a well developed, and regular, lingual ornament and by the presence of more gracile root branches.

Genus SCAPANORHYNCHUS Woodward, 1889

Scapanorhynchus praeraphiodon Sokolov, 1978 ? *sensu* Biddle, 1993

Text-Figure 6, C-F

Material. Two identifiable specimens, LIVCM 1998. 20. BT-BS; isolated cusps probably assignable to this taxon are frequent.

Horizon and localities. Speeton: Hunstanton Formation, Weather Castle Member, beds WC 2 and WC 3 (upper Upper Albian). Isolated cusps assignable to this species are present throughout the Hunstanton Formation at South Ferriby and more rarely within the Dulcey Dock and Weather Castle Members at Speeton.

Description. The main cusp is high and slender, with a narrow, but well developed, cutting edge. The labial face is almost flat, the convexity of the lingual face being greater in the anterior teeth than in the laterals. Ornament is restricted to a series of slight folds in the lower third of the lingual face. These are more strongly developed and straighter in the lateral teeth. A pair of small lateral cusplets is present on a poorly developed crown tongue. The root branches are strongly divergent, and a strong lingual protuberance is present in the anterior teeth. The nutritive groove is strongly developed.

Remarks. The specimens figured here correspond very closely to the teeth figured as ?*Scapanorhynchus praeraphiodon* by Biddle (1993), although it is unclear whether this is synonymous with *Scapanorhynchus praeraphiodon sensu* Sokolov, 1978, as the taxonomy of this taxon is confused by poorly preserved type material and incorrect referral of subsequent specimens (Siverson 1992, Biddle 1993). This is further complicated by the possible synonymy with *Carcharias tenuis* (Davis, 1890), which is discussed in detail by Siverson (1992). As the authors have not studied the type material involved, further comment cannot be made here.

Family CRETOXYRHINIDAE Glückman, 1958

Genus PSEUDISURUS Glückman, 1957 *sensu* Siverson, 1996

Pseudisurus sp.

Text-Figure 6, I

Material. One poorly preserved specimen, LIVCM 1998. 20. BW.

Horizon and localities. Speeton: Hunstanton Formation, Weather Castle Member, bed WC 4 (upper Upper Albian).

Description. The single specimen has a straight, robust principal cusp with somewhat convex cutting edges and a short and robust triangular lateral cusplet. This is the largest tooth found in the Hunstanton Formation, with a crown length of 21mm.

Genus CRETOXYRHINA Glückman, 1958

Cretoxyrhina mantelli (Agassiz, 1843) ?

Text-Figure 6, J

Material. Two crowns, LIVCM 1998. 20. BX.

Horizon and localities. Speeton: Hunstanton Formation, Red Cliff Hole Member, bed RCH 1a/b (lower Lower Cenomanian).

Description. The unornamented cusp is elongate and straight sided, flaring at the base to form short lateral blades. The cusp is biconvex but rather compressed, with no ornament other than a slight groove near the base of the lingual face. The preserved lateral flare of the crown has a compressed, incipient cusplet at the end.

Remarks. Although present only as isolated cusps, the shape of the cusp and blade-like form of the lateral cusplets allow probable referral to this species.

Genus LEPTOSTYRAX Williston, 1900 *sensu* Cappetta, 1987

Leptostyrax sp.

Text-Figure 6, G-H

Material. Two rather poorly preserved teeth and numerous isolated cusps of similar morphology, LIVCM 1998. 20. BV.

Horizon and localities. Speeton: Hunstanton Formation, Dulcey Dock Member, bed DD 19 and Weather Castle Member, bed WC 6 (upper Upper Albian).

Description. Each tooth consists of a short main cusp with (probably) a single pair of robust lateral cusplets over a bulbous root. The main cusp is straight and weakly convex labially, but more strongly so labially. The cutting edge is well developed on both this and the single preserved lateral cusplet. The lateral cusplet is of a similar shape to the main cusp, and over half its length, but is inclined in a slightly more labial plane. The basal third of the cusps is ornamented on the labial side by small folds. These are sharp-edged, irregular and occasionally bifurcate. Ornament on the lingual face is restricted to a few very fine, parallel ridges. The root is not well preserved on any specimen, but is obviously robust and swollen lingually. There is no sign of a nutritive groove.

Remarks. Although *Leptostyrax* has often been recorded from the Albian of Europe (e.g. Biddle 1993), these specimens differ form the type material, and probably represent a species of *Protolamna* (Cappetta 1987). These Hunstanton Formation specimens more closely resemble the type material of *Leptostyrax* in both crown and root morphology, and as such represent the earliest European occurrence of *Leptostyrax sensu* Cappetta, 1987.

Genus cf. PROTOLAMNA Cappetta 1980*b*

cf. *Protolamna* sp.

Plate 7, Figures 6-8.

Material. One well preserved tooth, LIVCM 1998. 20. AY.

Horizon and localities. South Ferriby: Hunstanton Formation, bed 5b (lower Upper Albian).

Description. The main cusp is relatively short but sharp, with well developed cutting edges and is inclined slightly to the rear. The labial face is slightly convex, becoming flat at the base; the lingual face remaining convex throughout, especially towards the base. The single pair of lateral cusplets are relatively well developed and are in the same plane as the main cusp. Ornament is developed as a series of short and widely spaced sharp-edged folds, some bifurcate, on the basal part of the labial face of all cusps. The lingual face is unornamented. The root is large and strongly bilobate. The basal face is slightly concave and with a very prominent nutritive groove with a foramen at the lingual end. The margins of the basal face, especially lingually, are strongly marked by small foramina. The root lobes are long and rounded terminally, but are strongly flattened.

Remarks. This species has a similar overall morphology to *Protolamna sokolovi* Cappeta 1980*b*, but differs from it in several aspects of crown and root morphology, having a stronger crown ornament, flatter lingual face to the root and a wider nutrititive groove. It shows stronger overall similarities to *Pseudodontaspis herbsti* Case 1987 from the American Campanian, from which it differs in the possession of uncontorted lateral cusps and an unornamented nutritive groove. Additional material is required before this species could be fully described and its affinities known.

Family indet.

Plate 7, Figure 9

Material. Several hundred isolated and broken cusps, LIVCM 1998. 20. AZ.

Horizon and localities. Many levels at Speeton and especially common at all sampled horizons at South Ferriby.

Description. Although many of the isolated lamniform cusps fall within the range of morphology of the taxa described above, many possess morphologies suggesting the presence of other taxa. These are generically indeterminate and could represent species of genera such as *Eostratolamia*, *Paranomotodon*, *Carcharias* and *Archaeolamna*. Although variable in morphology, many of these isolated cusps (ranging from 1 to 5 mm in height) show a gracile cutting/piercing morphology and are either unornamented or possess a faint series of ridges on the labial face.

Order CARCHARHINIFORMES Compagno, 1973

Remarks. Scyliorhinids and similar teeth are generally uncommon, but the material present suggests a low abundance, high diversity fauna. As well as the species described below, there are several poorly preserved crowns that do not appear to belong to any of those species. It is therefore probable that the true 'scyliorhinid' diversity was even higher.

Family SCYLIORHINIDAE Gill, 1862 ?

Scyliorhinidae ? gen. indet

Plate 7, Figures 10-12

Material. One ?anterior tooth, complete except for some exfoliation to labial face, LIVCM 1998. 20. BA.

Horizon and localities. Speeton: Ferriby Formation, Crowe's Shoot Member, about 0.5 m above base (lower Lower Cenomanian).

Description. A very small tooth, 1mm wide, the affinities of which are unclear. The labial face of the crown is flat with a concave basal edge which overhangs the root, and appears to be unornamented. There is a robust principal cusp which is round in section and ornamented with five fine ridges on the lingual side. This is flanked by two pairs of well developed lateral cusplets. The inner pair are rather elongate and bear the same ornament as the principal cusp. The outer pair are more triangular in profile and have a weak cutting edge. They are unornamented and slightly curved labially. The shallow root is hemiaulacorhize, with the nutritive groove closed over lingually, but open labially. The strongly divergent root branches are poorly developed and flat based.

Remarks. This tooth is closest in respect to its morphology to those of members of the scyliorhinidae, but bears little resemblance to any known scyliorhinid genus. The labial crown overhang may suggest orectolobid affinities, and it is possible that this represents a morphology intermediate between the hemiscylliidae and parascylliidae, but these affinities will probably not be clarified until more material is obtained.

Genus PROTOSCYLIORHINUS Herman, 1977

Protoscyliorhinus sp.?

Plate 8, Figures 1-3

Material. Eight incomplete teeth, LIVCM 1998. 20. BB-BC.

Horizon and localities. Speeton: Hunstanton Formation, Queen Rocks Member bed QR7 and Speeton Beck Member, bed SB 6 (lower Upper Albian). South Ferriby: Hunstanton Formation, bed 6a (lower Upper Albian).

Description. The teeth are all very small, up to 0.9 mm in crown height. The crown consists of a single cusp above the narrow crown tongues. The triangular cusp is slender, elongate and flattened at the tip, but with a deep lingual face basally. In the more anterior teeth, the crown widens steadily from the cusp along the crown tongues with no lateral cusplets or shoulders. In more lateral teeth, poorly developed shoulders may be present, especially on the distal side. A cutting edge is present almost to the base of the crown tongues. The crown is unornamented, other than occasional incipient ridges on the basal part of the labial face. The root is poorly preserved in all specimens, but appears hemiaulacorhize.

Remarks. These teeth are referred to *Protoscyliorhinus* because of their overall similarity to laterally compressed teeth of *P. lamaudi* Biddle and Landemaine 1988. It is possible, however, that these teeth represent a genus of parascylliid, but the available material is not sufficiently well preserved to clearly resolve the affinities of this species.

Family SCYLIORHINIDAE Gill, 1862

Remarks. The generic affiliation of most Mesozoic scyliorhinids is very poorly known, and the majority have been placed within the extant genus *Scyliorhinus* de Blainville, 1816. So far, reassignment to other genera has been hampered by the lack of information on the dentitions of modern scyliorhinids (Halter 1994).

Genus SCYLIORHINUS de Blainville, 1816 sensu lato

'Scyliorhinus' dubius (Woodward, 1889)

Plate 8, Figure 4

Material. Two anterior tooth crowns, LIVCM 1998. 20. BD.

Horizon and localities. Speeton: Hunstanton Formation, Queen Rocks Member, bed QR7 (lower Upper Albian) and Ferriby Formation bed SLC11C (lower Middle Cenomanian).

Description. The principal cusp is elongate and accompanied by at least one elongate, but gracile, lateral cusp. Poorly developed cutting edges are present on both cusps. There is almost no ornament.

Remarks. Despite the poor preservation, these specimens compare favourably with the anterior tooth of the holotype specimen (Cappeta 1977*a*; fig.5).

Genus CRETASCYLIORHINUS gen. nov.

Derivation of name. From the common and widespread occurrence of this genus in Cretaceous rocks.

Type species. *Scyliorhinus destombesi* Cappetta, 1977*b*.

Diagnosis. Scyliorhinid teeth of generally robust form. Crown of main cusp and a single pair of well developed lateral cusplets which is relatively symmetrical in both anterior and lateral teeth. Main cusp short and robust, only slightly oval in cross section with poorly developed cutting edges. Lateral cusps similar and very weakly divergent. Labial ornament usually present as straight, regularly spaced folds which occasionally bifurcate towards base of crown and reach almost to the cusp apex. Lingual ornament absent or as fine ridges. Crown strongly overhangs root labially. Root compact and flat-based with flared lateral lobes to give basal face a 'heart shaped' profile. Vascularisation hemiaulacorhize with nutritive groove covered, except for distinct notch at labial end.

Remarks. *Cretascyliorhinus* is distinctly different to *Scyliorhinus*, from which it may readily be separated by the presence of well developed lateral cusplets on lateral teeth and absence of a massive lingual root protuberance (Halter 1994). It cannot be readily accommodated into any of the extant scyliorhinid subfamilies, and thus probably represents an extinct group. At present *Scyliorhinus destombesi* Cappetta, 1977b and *S*. cf. *destombesi* of Müller and Diedrich, 1991 and *S*. aff. *destombesi* Müller, 1989 are referred to *Cretascyliorhinus*, thus this genus ranges from Lower Albian to Campanian.

Cretascyliorhinus destombesi (Cappetta, 1977*b*)

Material. 36 teeth, ranging from well to poorly preserved, LIVCM 1998. 20. BE-BF.

Horizon and localities. Speeton, Speeton Clay, basal bed A1 (Lower Albian) to Hunstanton Formation, Red Cliff Hole Member, bed RCH 4a (lower Lower Cenomanian). South Ferriby: Hunstanton Formation, beds 3/4 to 6b (lower Upper Albian).

Description. Teeth with a rather robust principle cusp and a single pair of well developed lateral cusplets. The ornament is variable, but generally consists of prominent widely-spaced longitudinal ridges on both faces, especially the labial face, of all cusps. These ridges rarely bifurcate, except at the extreme base of the crown. In some smaller teeth, these may be largely absent on the main cusp. The root is rather massive and hemiaulacorhize. The basal face is flat and flared, especially so on the short root branches.

Genus PARASYMBOLUS Candoni, 1993

Parasymbolus reticularis sp. nov.

Plate 8, Figures 8-13

Derivation of name. From the reticulate ornament on the labial face of the crown.

Holotype. LIVCM 1998. 20. BJ.

Stratum typicum. South Ferriby: Hunstanton Formation, bed 6a (lower Upper Albian).

Referred material. Five teeth, four fairly well preserved, LIVCM 1998. 20. BG-BH, LIVCM 1998. 20. BK.

Horizon and localities. South Ferriby: Hunstanton Formation, beds 5b, 6a and 6b/7 (lower Upper Albian).

Diagnosis. Crown with main cusp and single pair of lateral cusplets. Shoulders suggestive of an incipient second pair of lateral cusplets may be present. All cusps are robust and biconvex with a well developed cutting edge. Labial ornament is strong, with four to six main folds on the main cusp, and two or three on the laterals which reach almost to apex. Basally, the folds bifurcate and form reticulate patterns across the width of the tooth. The lingual ornament consists of three to six fine ridges on the main cusp, up to three on the lateral cusplets, which rarely bifurcate. The base of the crown is broad and overhangs the root labially. The root is low and flat-based, with a well developed lingual bulge. the root lobes strongly are divergent and flared with a flared base at labial end bearing large basal foramina. The nutritive groove is open labially, but covered lingually in adults, and is probably open in juveniles.

Description. These small (up to 1.1 mm wide) teeth are very distinctive due to the strong ornament and flared root lobes. The triangular principal cusp is flanked by a single pair of prominent lateral cusps of similar shape, which, in some specimens, have a shoulder or incipient outer lateral cusp on either the mesial or posterior side. In some specimens one of the lateral cusps is poorly developed and rather rounded. There is a well developed cutting edge along the occlusal edge of the tooth, reaching to the top of the root laterally. The ornament is strong on the labial face of the cusps, with spaced, sharp-edged folds reaching almost to the tip of both the main and lateral cusplets. Towards the base, this ornament bifurcates in an irregular manner, connecting the ridges to form a continuous band of reticulation across the base of the labial face of the crown. This reticulation is less evident in the juvenile tooth. Ornament on the lingual faces consists of regularly spaced fine ridges extending to the tips of the cusps, but rarely bifurcating. The root is low but with a broad basal face that is flared below the lingual boss and below the extremities of the root branches. Although hemiaulacorhize, the nutritive groove is only closed over along its lingual half. An imperfectly preserved root of a juvenile tooth (0.5 mm wide) shows a completely open nutritive groove. Small foramina are abundant along the labial and lingual faces of the root.

Remarks. The genus *Parasymbolus* Candoni, 1993 was erected for *P. octevillensis* Candoni 1993 from the French Upper Jurassic. *Parasymbolus reticularis* sp. nov. very closely resembles the type species in overall morphology of the crown and root, as well as in possessing a similar ornament of sharp-edged ridges on the labial face of the crown and fine ridges on the lingual face. *P. reticularis* sp. nov. differs from *P. octevillensis* largely in possessing a generally lower and wider crown with a reticulate ornament at the base of its labial face. The root vascularization principally differs in that the nutritive groove is closed over in juveniles of *P. octevillensis*. The presence of *P. reticularis* sp. nov. gives this genus an extended range from Kimmeridgian to Albian. Scyliorhinids probably referable to *Parasymbolus* are also present in British Oxfordian and Bathonian sediments (CJU pers. obs.), suggesting that it was a long-lived genus ranging throughout Middle Jurassic to Lower Cretaceous.

Genus PTEROSCYLLIUM Cappetta, 1980*a*

Pteroscyllium ornatum sp. nov.

Plate 9, Figures 1-9

Derivation of name. From the ornate ornament on the teeth.

Holotype. LIVCM 1998. 20. BL.

Stratum typicum. Speeton: Hunstanton Formation, Weather Castle Member, bed 1 (lower Lower Cenomanian).

Referred material. 10 poorly to well preserved teeth, LIVCM 1998. 20. BM-BP.

Horizon and localities. Speeton: Hunstanton Formation, Speeton Beck Member, bed SB 1 (lower Upper Albian) to Red Cliff Hole Member, bed RCH 1c (lower Lower Cenomanian). South Ferriby: Hunstanton Formation, beds 5b and 6a (lower Upper Albian).

Diagnosis. Relatively heterodont with a single pair of prominent lateral cusplets. Cusps strongly biconvex with well developed cutting edges. Strong labial ornament of spaced bifurcating folds reaching almost to the apex of the cutting edge. Finer lingual ornament of spaced and discontinuous longitudinal ridges, only rarely bifurcating. The root is large with wide nutritive groove and somewhat concave basal face.

Description. This species includes the largest scyliorhinid teeth recovered during this study (up to more than 4.5 mm high). The tooth shape varies from as wide as high in lateral teeth to the height being 2.5 times the width in anterior teeth. The principal cusp is robust but sharply pointed, and often curved posteriorly, and a single pair of large lateral cusplets, generally of equal size. There is a very strong cutting edge over all three cusps. The labial face of the crown is ornamented with prominent, somewhat sinuous, longitudinal folds which reach almost to the cusp tips and generally bifurcate towards the base. The lingual face is ornamented with weaker, more closely spaced ridges which are discontinuous and rarely bifurcate. The root is low with a rather concave basal face. The root branches are variable in length, but are rarely wider than the crown and are oval in cross section. Vascularisation is holoaulacorhize, with a well developed nutritive groove. Small foramina are abundant across the root.

Remarks. *Pteroscyllium* was initially defined on complete complete skeletal remains with well preserved dentitions of two species from Lebanese Santonian sediments (Cappetta 1980*a*). The teeth of *P. ornatum* are similar in overall morphology to the teeth of the

Lebanese specimens, with the well developed lateral cusplets and strong and anastomosing labial crown ornament and the curved root basal face with very prominent nutritive groove. *P. ornatum* possesses a coarser and more widely spaced crown ornament than either of the Lebanese taxa, as well as having wider and flatter root branches than *P. dubertreti* Cappetta, 1980*a*, and a less prominent lingual root protuberance than *P. signeuxi* Cappetta, 1980*a*. *P. ornatum* resembles *P. nolfi* Müller and Diedrich 1991 from German Cenomanian chalks, but differs from it in several ways. The labial ridges of *P. nolfi* are more gracile and closely spaced than in *P. ornatum*, rarely reaching nearer the apex of the cusps and only occasionally bifurcating near the base of the crown. Lingual ornament of *P. nolfi* is stronger and the ridges more closely spaced and continuous, and the root branches of *P. nolfi* are generally less massive and with a narrower basal face than in *P. ornatum*. A poorly preserved specimen of *Pteroscyllium* from the Hythe Beds (Aptian) of southern England (Batchelor and Ward 1990) has very widely spaced labial ridges and may represent an undescribed species.

Galeomorphii *incertae sedis*

Plate 9, Figures 10-12

Material. Two imperfect teeth, LIVCM 1998. 20. BQ-BR.

Horizon and localities. Speeton: Hunstanton Formation, Weather Castle Member, beds WC 1 and WC 7 (upper Upper Albian).

Description. These teeth bear little resemblance to known Cretaceous taxa, but are too poorly preserved to serve as a basis for a new taxon. The teeth are small (to 1.7 mm high) and consist of a linguo-labially flattened crown above a rather featureless root of similar height. The crown consists of a principal cusp which seems to be curved labio-posteriorly, and a small, probably mesial, cusplet. In both specimens, the position of a potential second cusplet is broken. The root is massive and compressed and appears anaulacorhize. The supposed basal face is at a low angle to the crown, and the lingual face of the root in one specimen has a prominent foramen.

Remarks. The presence of more than one tooth of the same type in a relatively unfossiliferous unit suggests that this does not simply represent a malformed tooth. Among

Cretaceous selachians with an anaulacorhize root, none is known to have a crown of this morphology. Among living sharks, this general tooth shape (small, conical crown and massive root) is possessed by filter feeding taxa in which the root is secondarily anaulacorhize. It is possible therefore that these teeth represent a filter feeding species of unknown affinities.

Superorder BATOMORPHII Cappetta, 1980*a*
Order RAJIFORMES Berg, 1940
Family RHINOBATIDAE Müller and Henle, 1838-1841

Genus SQUATIRHINA Casier, 1947

Squatirhina thiesi Biddle, 1993

Text-Figure 7, A-E

Material. Ten complete and partial teeth including those of juveniles, LIVCM 1998. 20. BY-CA, LIVCM 1997. 51. G.

Horizon and localities. Speeton: Speeton Clay Formation bed A1A (lower Middle Albian) and Hunstanton Formation, Red Cliff Hole Member, bed RCH 3 (lower Lower Cenomanian). South Ferriby: Hunstanton Formation, beds 3/4, 5b and 6a (lower Upper Albian).

Description. In the teeth of adults the crown consists of an elongate cusp with a cutting edge only in lateral teeth. At the base the crown is flared laterally, and is distinctly pectinate along its labial edge with a sharply angled lingual edge. The labial apron is well developed and the root is high and strongly bifid with a large nutritive groove. The smallest teeth, presumably of juveniles, have a poorly developed cusp and labial apron, and a distinctly lozenge-shaped crown. In larger specimens the angled and pectinate lingual crown edge is reduced, while both the angled surface and pectination are absent in the smallest tooth. The roots of the juvenile teeth are low and have a flatter basal face and wider nutritive groove than in those of adults. As with the crown, in juveniles the root is compressed labio-lingually.

Remarks. The presence of teeth of a series of growth stages demonstrates how the unusual adult tooth morphology of *Squatirhina* develops from the smooth, broad teeth of juveniles. Thus the elongate cusp and pectinate lateral portions of the crown may be demonstrated to develop by elongation of the lingual edge of tooth of a more standard rhinobatid morphology.

Squatirhina ? sp.

Text-Figure 7, F-G

Material. One incomplete tooth, LIVCM 1998. 20. CJ.

Horizon and localities. Speeton: Hunstanton Formation, Red Cliff Hole Member, bed RCH 1F (lower Lower Cenomanian).

Description. This tooth somewhat resembles the adult teeth of *Squatirhina thiesi* (Biddle 1993), but is considerably smaller (0.55 mm wide as opposed to 1-1.5 mm wide in *S. thiesi*). The cusp is elongate and deep with a weak cutting edge. At its base, the crown has wide lateral expansions that are somewhat pectinate on both labial and lingual edges, almost developing into incipient lateral cusps. There is a strongly angled edge connecting the apex of this expansion and the cutting edge of the cusp. The labial apron is wide and shallow, and there is a narrow enameloid-covered lingual boss. The holoaulacorhize root is distinctly ‘v’-shaped and extends laterally as far as the edge of the crown. The basal face is flat and rather flared, with a large foramen in the centre of the preserved root lobe.

Remarks. In some respects this tooth resembles *Squatirhina thiesi*, but is sufficiently different as to represent a separate, related species. The laterally expanded, denticulate crown is similar to that possessed by adult lateral teeth of *S. thiesi*, although somewhat more linguo-labially compressed. These features are not, however, differentiated in *S. thiesi* teeth of this size. The flat basal face of the root is seen only in juveniles of *S. thiesi*, and so it is possible that this is a juvenile of a *Squatirhina* or similar genus, with very ornate teeth and for which adults are still unknown. The general morphology of the tooth, in particular the rather crusiform crown, also resembles teeth of some genera of sclerorhynchoids such as *Ischyrhiza* and *Onchopristis*. Despite this, the pectinate crown ornament differs from that recorded on any sclerorhynchoid tooth, and thus this affinity seems unlikely.

Family SCLERORHYNCHOIDEI Cappetta, 1980*a*

Sclerorhynchoide gen. et sp. indet.

Text-Figure 7, H-I

Material. Two exfoliated rostral teeth (LIVCM XXXX).

Horizon and localities. Speeton: Hunstanton Formation, Queen Rocks Member, bed QR5 (lower Upper Albian) and Red Cliff Hole Member, bed RCH 4a (lower Lower Cenomanian).

Description. A small rostral tooth, 1.3 mm high. The cusp is rather compressed with a weakly sigmoidal curvature. There is a weak cutting edge and a pair of parallel ridges on the ?distal margin. The base of the cusp has exfoliated, but it appears that enameloid originally extended to the top of the root. The basal face of the root is flared and flat, being oval in outline. The upper face of the root has many small foramina.

Remarks. The generic affinities of this rostral tooth are unclear. The small size and general shape of the crown bear a resemblance to rostral teeth of several genera such as *Libanopristis* Cappetta, 1980*a*, *Micropristis* Cappetta, 1980*a* and some smaller species of *Ischyrhiza* such as *I. viaudi* Cappetta 1981. The flared root, however, is unlike that of any described taxon, and it is thus likely that these rostral teeth belong to an as yet undescribed genus. Sclerorhynchoids are well known from Albian (e.g. Thurmond 1971) and Cenomanian (e.g. Cappetta 1980*a*) sediments, but these early occurrences are restricted to areas of strong tethyan influence, the earliest recorded sclerorhynchoid rostral teeth from boreal northern Europe being Santonian in age (Herman 1977). These remains from the Hunstanton Formation thus represent the oldest known occurrence of boreal sclerorhynchoids.

OTHER SELACHIAN MATERIAL - DENTICLES

Remarks. All of the denticles recovered exhibit a fairly simple ‘placoid’ morphology (Reif 1978). Other forms of dermal bone (such as dermal thorns or fin spines) or hybodont-type denticles were not found. Denticle terminology is based on Duffin and Ward (1993).

Denticle type 1

Text-Figure 8, A

Material. One imperfect specimen, LIVCM 1998. 20. CC.

Horizon and localities. Speeton: Hunstanton Formation, Queen Rocks Member, bed QR 3 (lower Upper Albian).

Description. The crown is elongate, widening rapidly from the anterior edge and then smoothly tapers towards the apex, which is missing. There are nine straight, faint longitudinal ridges which fade out distally. The base is poorly preserved, but there is a slender vertical neck below the anterior part of the crown and a rather small ?tetraradiate base.

Denticle type 2

Text-Figure 8, B-C

Material. 20 specimens, LIVCM 1998. 20. CD-CE.

Horizon and localities. Speeton: Speeton Clay Formation bed A1A (lower Middle Albian) to Hunstanton Formation, Red Cliff Hole Member, bed RCH 5c (lower Lower Cenomanian). South Ferriby: Hunstanton Formation, bed 6a (lower Upper Albian).

Description. The crown has a relatively pointed anterior end, in some cases with a pair of small indentations either side of the origin of the central keel. The distal apex is sharply pointed and often has a pair of small lateral points. The surface is ornamented by several strong longitudinal ridges, which run from the proximal to distal edges. The central ridge is either flat topped or with a central indentation, whilst the one, or less often two, pairs of lateral ridges are sharp edged. The neck is robust and leads to a wide tetraradiate base.

Denticle type 3

Text-Figure 8, D

Material. One specimen, LIVCM 1998. 20. CF.

Horizon and localities. Speeton: Hunstanton Formation, Red Cliff Hole Member, bed RCH 5c (lower Lower Cenomanian).

Description. This is the largest denticle recovered, being about 450 μm across. The crown is inclined to the basal plate at about 60 degrees, and has a convex surface. The anterior (curved) portion is ornamented by five strong, parallel ridges, which fade out distally to give a flat posterior portion. The apex is blunt with some suggestion of lateral points or shoulders. There is no true neck, merely a constriction, and the base is wider than the crown.

Denticle type 4

Text-Figure 8, E

Material. Two specimens, LIVCM 1998. 20. CG.

Horizon and localities. Speeton: Hunstanton Formation, Queen Rocks Member bed QR3 and Dulcey Dock Member, bed DD 6 (lower Upper Albian).

Description. The rather asymmetrical crown is strongly convex on its proximal edge, but less so distally. The apex is flanked by two lateral points, all three points occurring at the end of an extremely strong, sharp edged, ridge which runs in parallel to each other for the length of the crown. Over much of the crown, especially proximally, there is a fine and very regular ornament of small polygonal pits, each about 10 μm across. The base is not preserved.

Denticle type 5

Text-Figure 8, F

Material. Two specimens, LIVCM 1998. 20. CH.

Horizon and localities. South Ferriby: Hunstanton Formation, bed 6a (lower Upper Albian).

Description. The crown is rounded, being angled anteriorly and rounded posteriorly. It is thick, unornamented and the posterior edge is angled upwards. The root is high and tetraradiate, flaring steadily from the base of the crown to a flat base.

Possible assignment of denticles

The assignment of denticles to particular taxa is fraught with difficulties due to their generally conservative morphology and the degree to which they vary over the body of an individual fish (e.g. Cappetta 1987). When compared to material from known Cretaceous taxa , denticle type 1 is similar to denticles from squalids (Cappetta 1980*a*, pl. 5, fig. 7), orectolobids (Cappetta 1980*a*, pl. 17, fig. 4) and scyliorhinids (Cappetta 1980*a*, pl. 20, fig. 4). Evidently this is simply a generalized denticle morphotype used in streamlining. Denticle type 2 is very similar to specimens figured for *Hexanchus* (Cappetta 1980*a*, pl. 1, fig. 3) and *Synechodus dubrisiensis* (Duffin and Ward 1993, text-fig. 12, h-i), and Jurassic material referred to *Synechodus* (Thies 1995) and probably represents a mixed suite of synechodontiform (*sensu* Duffin and Ward 1993) scales. Denticle type 3 is, in most respects a more robust version of denticle type 2, and may simply be a scale from a more exposed part of the body of the same type of fish. This type bears a strong resemblance to a denticle from the dorsal margin of the tail of a specimen of *Synechodus* form the Lower Jurassic (Duffin and Ward 1993, text-fig. 9, k). The general morphology of type 4 is again rather cosmopolitan, but the distinctive ornament is very similar to that of denticles of *Pteroscyllium* (Cappetta 1980*a*, pl. 23, figs 9-10). Denticle type 5 has the most robust morphology, and was presumably positioned in an area of maximum skin abrasion.

FAUNAL VARIATIONS AND COMPARISONS WITH OTHER LOCALITIES

The Albian to Cenomanian Cretaceous selachian faunas of Speeton and South Ferriby are generally similar, but differ in several ways. This may, in part, be due to stratigraphic factors such as the greater completeness of the section at Speeton, although even in parts of the succession where sampled levels are equivalent (the Queen Rocks to Dulcey Dock members of the Speeton succession are equivalent to the sampled part of the succession at South Ferriby), the faunas differ. The dominant faunal element at Speeton is *Protosqualus* (which comprises up to 70 per cent of the fauna at some horizons), a form relatively uncommon at South Ferriby. There is also a far greater frequency of *Notorhynchus* at Speeton, which remains common until at least the Middle Cenomanian. Scyliorhinids are also more abundant and diverse at Speeton. In contrast, the dominant elements of the South Ferriby fauna are the teeth of small lamniforms. These are relatively uncommon at Speeton, where larger lamniforms are restricted to occasional specimens in rocks immediately adjacent to the Albian-Cenomanian boundary. These occurrences coincide with a positive stable carbon isotope excursion (Mitchell 1995), which may be interpreted as a temporary increase in nutrient levels within the North Sea Basin watermass. The difference in faunas between the two localities is probably related to a combination of water depth and water mass nutrient levels, and hence differing quantity and types of potential prey items.

There is no compelling evidence for a temporal change in faunas at South Ferriby, although at Speeton such a change is present. Most of the commonest species at Speeton persist from the Albian portion of the Speeton Clay (upper A Beds) to the chalks of the basal Ferriby Formation, although the relative frequency of some taxa varies. There is very little difference in the faunas from the upper A Beds and the Queen Rocks and Speeton Beck members of the Hunstanton Formation. However, the faunas of the Dulcey Dock to Crowe's Shoot members are noticeably dissimilar. The most marked difference is the change in the frequency of *Protosqualus sigei*. This is by far the commonest species in the lower part of the succession (usually 50-70 per cent of the fauna) and, although still common, is far less frequent higher up (usually 20-40 per cent of the fauna). Larger lamniformes and *Pseudospinax* appear to be largely restricted to the upper part of the succession (text-fig 3-4). This faunal change coincides with a facies change from more carbonate-poor lithologies to more carbonate-rich lithologies. It is, possible therefore, that the change in selachian faunas was either indirectly substrate controlled (via a change in available food), or controlled by the same factors that let to the increase in carbonate production (such as a change in water depth or primary nutrient levels).

Selachian faunas from other Hunstanton Formation localities are very poorly known. Acid digestion of the shallow water limestones of Rifle Butts Quarry on the Market Weighton Structure has yielded fragmentary teeth probably referable to *Synechodus, Protosqualus* and *Squatina*. Fish remains are rare at Hunstanton (Le Strange 1974) at the southern limit of the Red Chalk facies, although ?*Hispidaspis* Sokolov, 1978 is present (SFM pers. obs), whilst collections from this site in the Sedgwick Museum, Cambridge, contain teeth of lamniforms and chimaeroid remains (CJU pers. obs.).

Faunas from the Gault Clay facies of southern England and northern France differ markedly from those of the Hunstanton Formation. *Notorhynchus* is rare in the Gault Clay of the English East Midlands (Smart 1995) and Kent (Ward, pers. comm.) and was not recorded in northern France in a study by Biddle (1993). Gault Clay faunas are dominated by medium to large lamniforms and contain groups such as hybodonts, *Ptychodus*, anacoracids, *Spathobatis* and chimaeroids not recorded from the Hunstanton Formation.

Conversely, the Gault Clay facies contains few small benthic taxa, with squalids, scyliorhinids and hemiscylliids being uncommon and of low diversity. The Cambridge Greensand of the English East Midlands, a hiatal deposit at least partly of Albian age, contains a rich selachian fauna. Collections in the Sedgwick Museum, Cambridge, and British Geological Survey Museum, Keyworth, contain numerous *Notorhynchus* and chimaeroids in a fauna dominated by medium to large lamniforms (CJU pers, obs.). Unfortunately, no studies of the smaller teeth have been published.

The Cenomanian of northern Germany contains a fauna which is in many ways intermediate between the Hunstanton Formation and the Gault Clay faunas. It contains abundant and diverse scyliorhinids, squalids and orectolobids associated with numerous small to large lamniformes (Müller and Diedrich 1991). Although further removed stratigraphically and geographically from the Hunstanton Formation than Gault Clay sections, northern Germany was within the same North Sea Basin as North East England during the Cretaceous (Mitchell 1996*b*).

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(All text-figures and plates are at publication size except TEXT-FIG.1 and 7., which will need reducing to page size)

EXPLANATION OF PLATE 1.

Figs 1-5. *Synechodus dubrisiensis* (Mackie, 1863); Hunstanton Formation. 1, LIVCM 1998. 20. A, anterolateral tooth, labial view, South Ferriby, bed 5b, width 1.5 mm. 2, LIVCM 1998. 20. B, posteriolateral tooth, labial view, Speeton, bed QR7, preserved width 1.8 mm. 3-5, LIVCM 1998. 20. C, ?parasymphyseal tooth, Speeton, bed RCH4a, width 1.2 mm, 3, lateral view, 4, labial view, 5, lingual view.

Fig. 6. *Synechodus nitidus* Woodward, 1912; Hunstanton Formation. LIVCM 1998. 20. D, lateral tooth, labial view, South Ferriby, bed 6a, width 3.5 mm.

Fig. 7. *Paraorthacodus recurvus* (Trautschold, 1877); Hunstanton Formation. LIVCM 1998. 20. E, anterolateral tooth, oblique labial view, Speeton, bed DD20, height 5 mm.

Figs 8-12. *Notorhynchus aptiensis* (Pictet, 1865); Hunstanton Formation. 8, LIVCM 1998. 20. F, immature upper anterolateral tooth (?UA-L 2 to 3), lingual view, South Ferriby, bed 6a, width 2.3 mm. 9, LIVCM 1998. 20. G, immature upper anterolateral tooth (?UA-L 4 to 6), lingual view, South Ferriby, bed 4 width 3.3 mm. 10, LIVCM 1998. 20. H, adult lower anterolateral tooth (L A-L 2 to 5), lingual view, Speeton, bed DD6, width 11.1 mm. 11, LIVCM 1998. 20. J, lower symphyseal tooth, labial view, Speeton, bed QR3, width 1.5 mm. 12. LIVCM 1997. 51. H, anterolateral tooth (?lower) of small juvenile, labial view, Speeton, bed WC1, width 1.2 mm.

EXPLANATION OF PLATE 2.

Fig. 1. *Hexanchus* sp. indet.; Ferriby Formation. LIVCM 1998. 20. K, partial lower anterolateral tooth, Speeton, bed SLC11C, preserved width 2 mm.

Figs 2-4. *Squalus* sp.; Ferriby Formation. 2. LIVCM 1998. 20. L, incomplete tooth, labial view, Speeton, Crowe's Shoot Member, preserved width 0.8 mm. 3-4. LIVCM 1998. 20. M, Speeton, bed SLC11C, width 0.83 mm, 3, labial view, 4, lingual view.

Figs 5-8. *Protosqualus sigei* Cappetta, 1977; Hunstanton Formation. 5, LIVCM 1998. 20. N, large posterior tooth, labial view, South Ferriby, bed 6a, width 2.8 mm. 6, LIVCM 1998. 20. P, lateral tooth, labial view, Speeton, bed SB12, width 1.3 mm. 7, LIVCM 1998. 20. Q, anterior tooth, lingual view, South Ferriby, bed 6a, width 1 mm. 8, LIVCM 1998. 20. R, anterolateral tooth, labial view, South Ferriby, bed 5b, width 0.9 mm.

Figs 9-11. *Protosqualus pachyrhiza* sp. nov.; Hunstanton Formation. LIVCM 1998. 20. S, holotype, anterior tooth, South Ferriby, bed 6a, width 1.4 mm, 9, lingual view, 10, labial view, 11, basal view.

EXPLANATION OF PLATE 3.

Figs 1-2. *Protosqualus pachyrhiza* sp. nov.; Hunstanton Formation. LIVCM 1998. 20. T, lateral tooth, South Ferriby, bed 6a, width 1.9 mm, 1, lingual view, 2, basal view.

Figs 3-6. Squalidae gen. indet. Hunstanton Formation. 3, LIVCM 1998. 20. U, incomplete tooth, labial view, Speeton, bed DD15, width 0.7 mm. 4-6, LIVCM 1998. 20. V, Speeton, bed WC2, width 1.2 mm, 4, lingual view, 5, labial view (specimen broken), 6, basal view.

Figs 7-8. *Eoetmopterus* ? sp.; Ferriby Formation. LIVCM 1998. 20. W, lower tooth, Speeton, bed SLC11C, width 1.45 mm, 7, labial view, 8, lingual view.

Fig. 9. Echinorhinid ? indet.; Hunstanton Formation. LIVCM 1998. 20. X, labial view, Speeton, bed DD16, preserved width 1.1 mm.

EXPLANATION OF PLATE 4.

Figs 1-2. *Squatina* cf. *cranei* Woodward, 1888b; Ferriby Formation. LIVCM 1998. 20. Y, lateral tooth, Speeton, bed SLC11C, width 4.9 mm, 1, labial view, 2, occlusal view.

Figs 3-4. *Squatina* sp. Hunstanton Formation. LIVCM 1998. 20. Z, lateral tooth, Speeton, bed WC1, width 1.2 mm, 3, labial view, 4, occlusal view.

Figs 5-8. *Heterodontus canaliculatus* (Egerton *in* Dixon, 1850) ?; Hunstanton Formation. 5, LIVCM 1998. 20. AA, anterior tooth, labial view, South Ferriby, bed 5b, height 2.15 mm. 6, LIVCM 1998. 20. AB, worn lateral tooth, occlusal view, South Ferriby, bed 2, preserved width 3.9 mm. 7-8, LIVCM 1998. 20. AC, juvenile anterolateral tooth, South Ferriby, bed 5b, width 2.1 mm, 7, lingual view, 8, labial view.

Fig. 9. *Chiloscyllium* cf. *greeni* (Cappetta, 1973); Hunstanton Formation. LIVCM 1998. 20. AD, incomplete ?anterior tooth, labial view, Speeton, bed WC2, height 1.3 mm.

Figs 10-12. cf. *Hemiscyllium* sp.; Hunstanton Formation. 10, LIVCM 1998. 20. AE, lateral tooth, labial view, Speeton, bed DD15, height 0.8 mm. 11, LIVCM 1998. 20. AF, ?anterolateral tooth, labial view, South Ferriby, bed 5b, height 1 mm. 12, LIVCM 1998. 20. AG, ?parasymphyseal tooth, labial view, South Ferriby, bed 6a, height 1 mm.

EXPLANATION OF PLATE 5.

Figs 1-2. cf. *Hemiscyllium* sp.; Hunstanton Formation. LIVCM 1998. 20. AH, anterior tooth, South Ferriby, bed 6a, height 1 mm, 1, labial view, 2, lateral view.

Figs 3-10. *Pseudospinax heterodon* sp. nov.; Hunstanton Formation. 3, LIVCM 1998. 20. AJ, 'small cusped' anterior tooth, oblique view, Speeton,DD6, width 0.65 mm. 4, LIVCM 1998. 20. AK, 'large cusped' anterior tooth, labial view, Speeton, bed RCH5c, width 0.6 mm. 5-7, LIVCM 1998. 20. AL, holotype, 'small cusped' lateral tooth, Speeton, bed DD7, width 0.76 mm, 5, posterior lateral view, 6, labial view, 7, anterior lateral view. 8. LIVCM 1998. 20. AM, 'small cusped' anterior tooth, labial view, Speeton, bed WC1, width 0.71 mm. 9, LIVCM 1998. 20. AN, 'large cusped' anterior tooth, labial view, Speeton, bed WC7, width 0.41mm. 10, LIVCM 1998. 20. AP, 'large cusped' lateral tooth, labial view, Speeton, bed RCH5c, width 0.65 mm.

EXPLANATION OF PLATE 6.

Fig. 1. *Orectoloboides parvulus* (Dalinkevicius, 1935) ?; Speeton Clay Formation. LIVCM 1998. 20. AQ, lateral tooth, oblique lateral view, Speeton, bed A5A. Preserved height 0.8 mm.

Figs 2-4. *Cretascyllium* sp.; Hunstanton Formation. LIVCM 1998. 20. AR, ?anterior tooth, Speeton, bed SB12, height 2.3 mm, 2, labial view, 3, lateral view, 4, lingual view.

Figs 5-9. *Cretorectolobus gracilis* sp. nov.; Hunstanton Formation. 5-6, LIVCM 1998. 20. AS, holotype, South Ferriby, bed 6a, height 0.7 mm, 5, labial view, 6, lateral view. 7, LIVCM 1998. 20. AT, labial view, Speeton, bed SB4, height 1.5 mm. 8-9, LIVCM 1998. 20. AU, South Ferriby, bed 6a, height 1.5 mm, 8, labial view, 9, lateral view.

EXPLANATION OF PLATE 7.

Figs 1-5. *Pararhincodon* cf. l*ehmani* Cappetta, 1980a; Hunstanton Formation. 1-2, LIVCM 1998. 20. AV, anterior tooth, Speeton, bed WC5, height 0.7 mm, 1, labial view, 2, posterior lateral view. 3-4, LIVCM 1998. 20. AW, anterolateral tooth, South Ferriby, bed 6a, height 1.2 mm, 3, labial view, 4, posterior lateral view. 5, LIVCM 1998. 20. AX, lateral tooth, posterior lateral view, South Ferriby, bed 6a, height 1.4 mm.

Figs 6-8. cf. *Protolamna* sp.; Hunstanton Formation. LIVCM 1998. 20. AY, anterolateral tooth, South Ferriby, bed 5b, height 2.7mm, 6, labial view, 7, lingual view, lateral view.

Fig. 9. indet. lamniform. LIVCM 1998. 20. AZ, typical specimen, lateral tooth, labial view, South Ferriby, Hunstanton Formation bed 4, preserved height 4.4mm.

Figs 10-12. scyliorhinidae ? gen. indet.; Ferriby Formation. LIVCM 1998. 20. BA. ?anterior tooth, Speeton, Crowe's Shoot Member, width 1 mm, 10, labial view, 11, lingual view, 12, lateral view.

EXPLANATION OF PLATE 8.

Figs 1-3. *Protoscyliorhinus* sp.?; Hunstanton Formation. 1, LIVCM 1998. 20. BB, lateral tooth, labial view, Speeton, bed QR7, preserved height 0.8 mm. 2-3, LIVCM 1998. 20. BC, anterior tooth, South Ferriby, bed 6a, preserved height 1 mm, 2, labial view, 3, lateral view.

Fig. 4. '*Scyliorhinus*' *dubius* (Woodward, 1889); Hunstanton Formation. LIVCM 1998. 20. BD, partial anterior tooth, labial view, Speeton, bed QR7, preserved height 0.9mm.

Figs 5-7. *Cretascyliorhinus destombesi* (Cappetta, 1977*b*); Hunstanton Formation. 5-6, LIVCM 1998. 20. BE, lateral tooth, Speeton, bed RCH1c, height 1.3 mm, 5, labial view, 6, lateral view. 7, LIVCM 1998. 20. BF, anterior tooth, labial view, Speeton, bed SB6, height 0.7 mm.

Figs 8-13. *Parasymbolus reticularis* sp. nov.; Hunstanton Formation. 8, LIVCM 1998. 20. BG, lateral tooth, lingual view, South Ferriby,bed 6a, width 0.84 mm. 9-10, LIVCM 1998. 20. BH, lateral tooth, South Ferriby, bed 5b, width 1.1 mm, 9, labial view, 10, lateral view. 11, holotype, LIVCM 1998. 20. BJ, lateral tooth, labial view, South Ferriby, bed 6a, width 0.78 mm. 12-13, LIVCM 1998. 20. BK, juvenile anterolateral tooth, South Ferriby, bed 6b/7, width 0.5 mm, 12, labial view, 13, lateral view.

EXPLANATION OF PLATE 9.

Figs 1-9. *Pteroscyllium ornatum* sp. nov.; Hunstanton Formation. 1-3, LIVCM 1998. 20. BL, holotype, lateral tooth, Speeton, bed WC1, height 2 mm, 1, labial view, 2, lingual view, 3, lateral view. 4-6, LIVCM 1998. 20. BM, anterolateral tooth, Speeton, bed QR7, height 1.3 mm, 4, labial view, 5, lingual view, 6, lateral view. 7-6, LIVCM 1998. 20. BN, anterior (?parasymphyseal) tooth, Speeton, bed SB4, height 2.1 mm, 7, labial view, 8, lateral view. 9. LIVCM 1998. 20. BP, partial anterior tooth, labial view, South Ferriby, bed 5b, preserved height 1.9 mm.

Figs 10-12. Galeomorph gen. et sp. indet.; Hunstanton Formation. 10. LIVCM 1998. 20. BQ, ?lateral tooth, ?oblique lateral/lingual view, Speeton, bed WC5, height 1.1 mm. 11-12, LIVCM 1998. 20. BR, ?anterior tooth, Speeton, bed WC1, height 1.6 mm, 11, ?labial view, 12, lateral view.

EXPLANATION OF TEXT-FIG. 1.

Locality map of Speeton and South Ferriby and their palaeogeographical 0435-410-Xrelationships (from Mitchell 1996*a*).

EXPLANATION OF TEXT-FIG. 2.

Lower part of the sampled succession at Speeton (Albian part of the Speeton Clay Formation and the Queen Rocks and Speeton Beck Members of the Hunstanton Formation) showing the horizons sampled and occurrences of selachian teeth, with key for all three range diagrams. Scale in metres.

EXPLANATION OF TEXT-FIG. 3.

Upper part of the sampled succession at Speeton (Dulcey Dock to Red Cliff Hole Members of the Hunstanton Formation and parts of the Ferriby Formation) showing the horizons sampled and occurrences of selachian teeth. Scale in metres.

EXPLANATION OF TEXT-FIG. 4.

Stratigraphic succession at South Ferriby showing the horizons sampled and occurrnces of selachian teeth within the Hunstanton Formation. Scale in metres.

EXPLANATION OF TEXT-FIG. 5.

Graph showing the relative sizes of specimens of *Protosqualus sigei* Cappetta 1977*b* from the Hunstanton Formation (East Midlands Shelf and North Sea Basin) and Gault Clay Formation (Anglo-Paris Basin).

EXPLANATION OF TEXT-FIG. 6.

A-B. *Anomotodon principalis* Biddle, 1993, non Cappetta, 1975; Hunstanton Formation. LIVCM 1998. 20. BS, Anterior tooth, Speeton, bed WC6, height 12 mm, A, lingual view, B, lateral view.

C-F. *Scapanorhynchus praerhaphiodon* Sokolov, 1978 ?; Hunstanton Formation. C-D, LIVCM 1998. 20. BT, lateral tooth, Speeton, bed WC2, preserved height 7.2 mm, C, lingual view, D, lateral view. E-F, LIVCM 1998. 20. BU, anterior tooth, Speeton, bed WC3, Height 10.5 mm, E, lingual view, F, lateral view.

G-H. *Leptostyrax* sp.; Hunstanton Formation. LIVCM 1998. 20. BV, anterior tooth, Speeton, Hunstanton Formation bed DD19, preserved height 5.5mm, G, labial view, H, lateral view.

I. *Pseudisurus sp*.; Hunstanton Formation. LIVCM 1998. 20. BW, lingual view, Speeton, bed WC4, preserved height 21 mm.

J. *Cretoxyrhina mantelli* (Agassiz, 1843)?; Hunstanton Formation. LIVCM 1998. 20. BX, lingual view, Speeton,bed RCH1a/b, preserved height 10 mm.

EXPLANATION OF TEXT-FIG. 7.

A-E. *Squatirhina thiesi* Biddle, 1993; Hunstanton Formation. A, LIVCM 1998. 20. BY, tooth of small juvenile, labial view, South Ferriby, bed 4, width 0.7 mm. B-C, LIVCM 1998. 20. BZ, juvenile tooth, South Ferriby, bed 6a, width 0.8 mm, B, labial view, C, lateral view. D, LIVCM 1998. 20. CA, adult lateral tooth, South Ferriby, bed 5b, width 1.3 mm. E, LIVCM 1997. 51. G, adult anterior tooth, Speeton, bed RCH3, width 1.1 mm.

F-G. *Squatirhina* ?sp.; Hunstanton Formation. LIVCM 1998. 20. CJ, ?juvenile tooth, Speeton, bed RCH1f, width 0.56 mm, F, labial view, G, lateral view.

H-I. Sclerorhynchoide gen. et sp. indet.; Hunstanton Formation. LIVCM 1998. 20. CB, rostral tooth, Speeton, bed RCH4a, height 1.3 mm, H, lateral (?anterior) view, I, dorsal view.

EXPLANATION OF TEXT-FIG. 8.

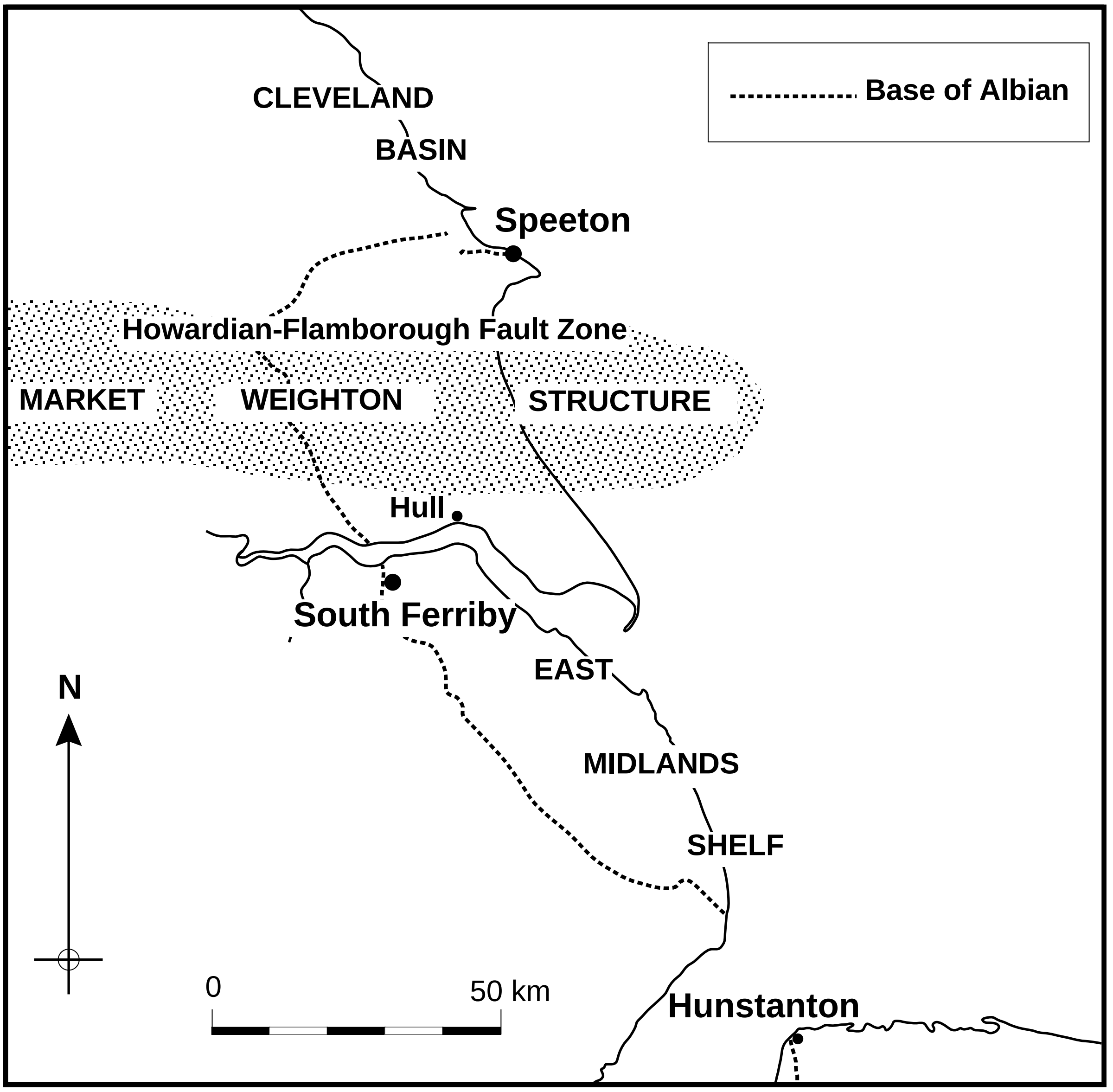
A. Denticle type 1. LIVCM 1998. 20. CC, surface view, Speeton, Hunstanton Formation bed QR3, crown length 0.4mm.

B-C. Denticle type 2. B, LIVCM 1998. 20. CD, anterior view, Speeton, Hunstanton Formation bed RCH5c, crown length 0.3mm. C, LIVCM 1998. 20. CE, surface view, Speeton, Hunstanton Formation bed DD6, crown length 0.5mm.

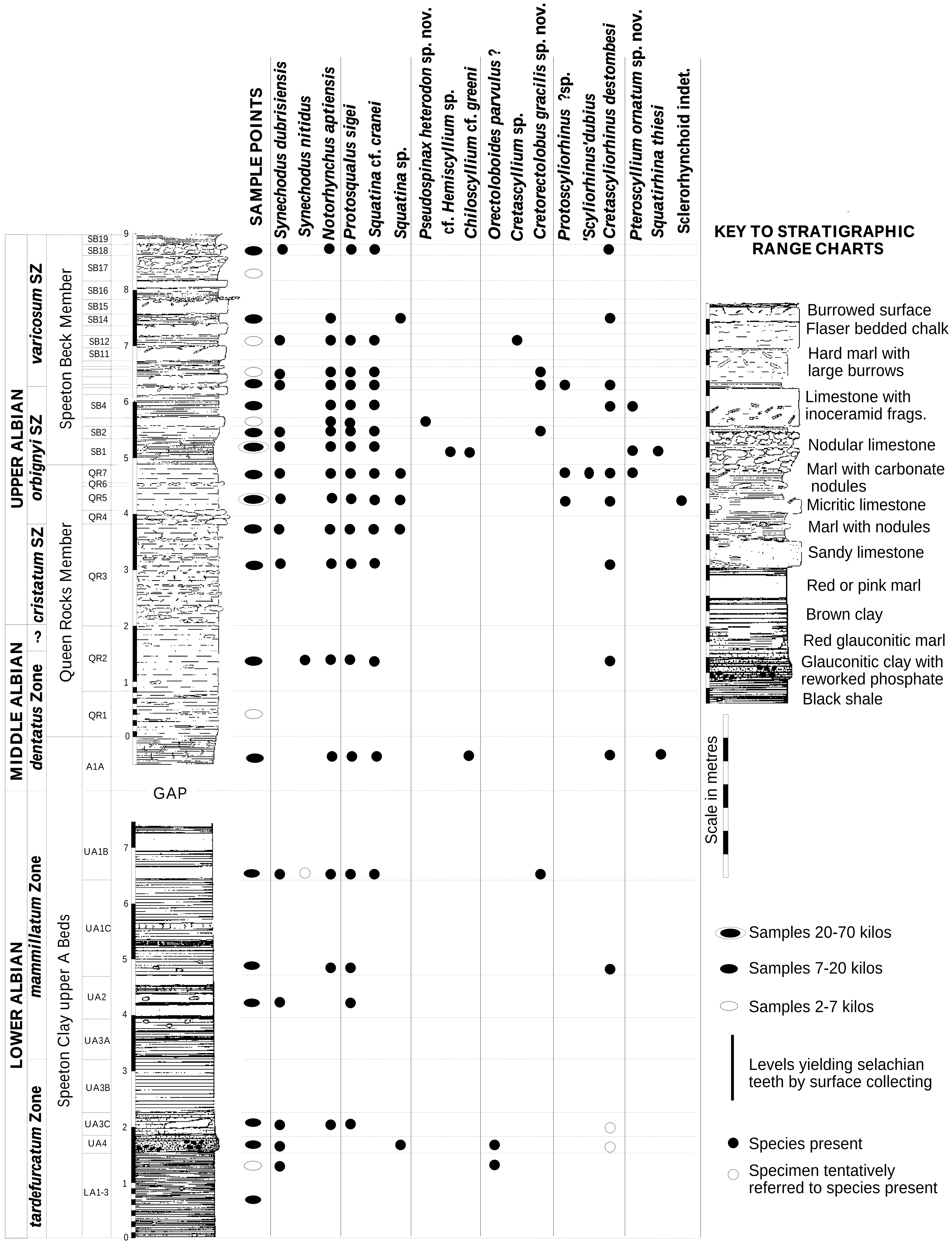
D. Denticle type 3. LIVCM 1998. 20. CF, anterior view, Speeton, Hunstanton Formation bed RCH5c, width 0.5mm.

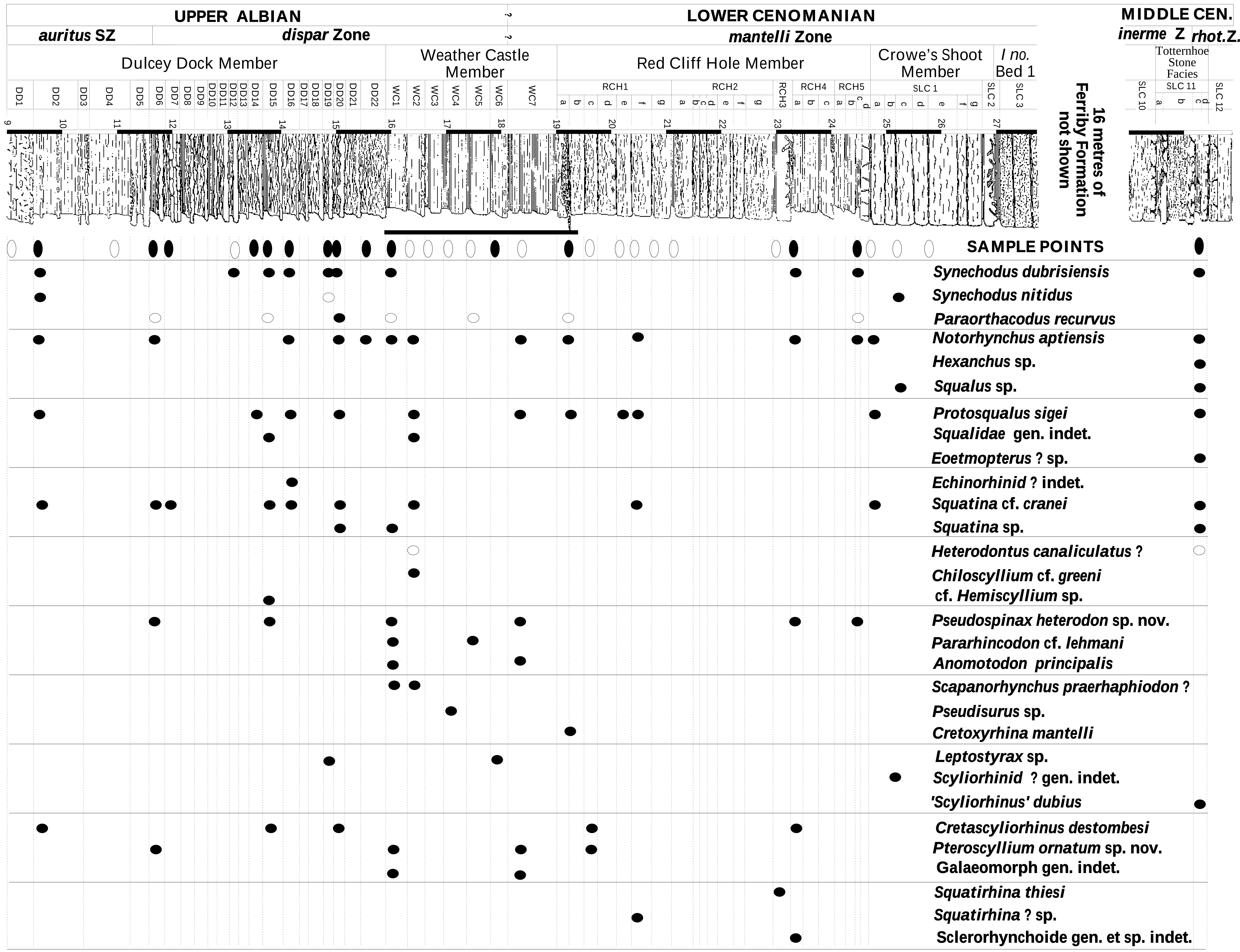
E. Denticle type 4. LIVCM 1998. 20. CG, oblique view, Speeton, Hunstanton Formation bed DD6, crown length 0.4mm.

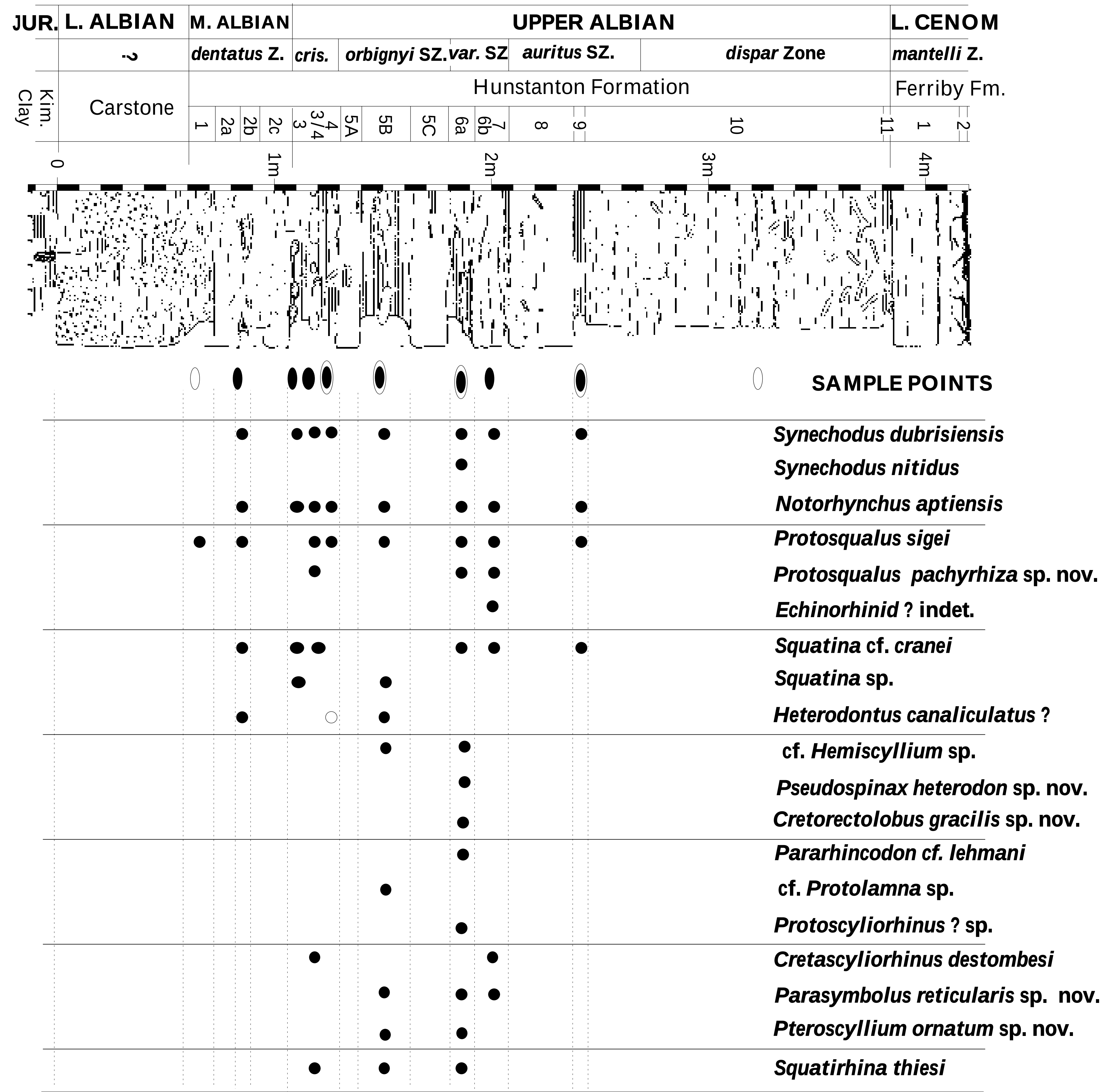
F. Denticle type 5. LIVCM 1998. 20. CH, oblique view, South Ferriby, Hunstanton Formation bed 6a, crown length 0.5mm.



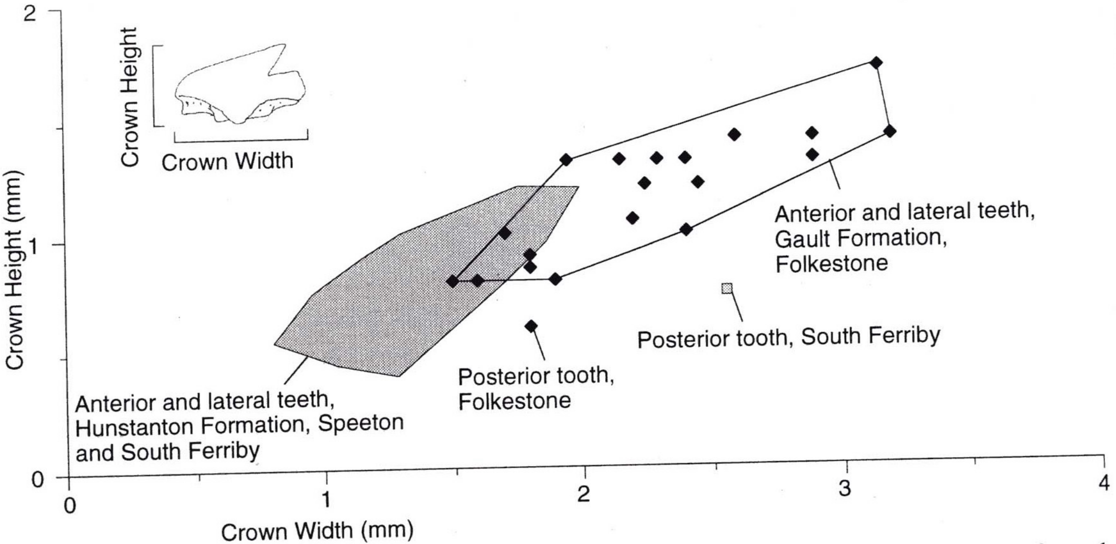
Base of Albian
CLEVELAND
BASIN
Speeton
Howardian-Flamborough Fault Zone
MARKET
WEIGHTON
STRUCTURE
Hull
South Ferriby
EAST
MIDLANDS
SHELF
N
0
50 km
Hunstanton


SAMPLE POINTS
Synechodus dubrisiensis
Synechodus nitidus
Notorhynchus aptiensis
Protosqualus sigei
Squatina cf. cranei
Squatina sp.
Pseudospinax heterodon sp. nov.
cf. Hemiscyllium sp.
Chiloscyllium cf. greeni
Orectoloboides parvulus ?
Cretascyllium sp.
Cretorectolobus gracilis sp. nov.
Protoscyliorhinus ?sp.
'Scyliorhinus'dubius
Cretascyliorhinus destombesi
Pteroscyllium ornatum sp. nov.
Squatirhina thiesi
Sclerorhynchoid indet.
UPPER ALBIAN
MIDDLE ALBIAN
LOWER ALBIAN
varicosum SZ
orbignyi SZ
cristatum SZ
?
dentatus Zone
mammillatum Zone
tardefurcatum Zone
Speeton Beck Member
Queen Rocks Member
Speeton Clay upper A Beds
SB19
SB18
SB17
SB16
SB15
SB14
SB12
SB11
SB4
SB2
SB1
QR7
QR6
QR5
QR4
QR3
QR2
QR1
A1A
UA1B
UA1C
UA2
UA3A
UA3B
UA3C
UA4
LA1-3
GAP
KEY TO STRATIGRAPHIC RANGE CHARTS
Burrowed surface
Flaser bedded chalk
Hard marl with large burrows
Limestone with inoceramid frags.
Nodular limestone
Marl with carbonate nodules
Micritic limestone
Marl with nodules
Sandy limestone
Red or pink marl
Brown clay
Red glauconitic marl
Glauconitic clay with reworked phosphate
Black shale
Scale in metres
Samples 20-70 kilos
Samples 7-20 kilos
Samples 2-7 kilos
Levels yielding selachian teeth by surface collecting
Species present
Specimen tentatively referred to species present

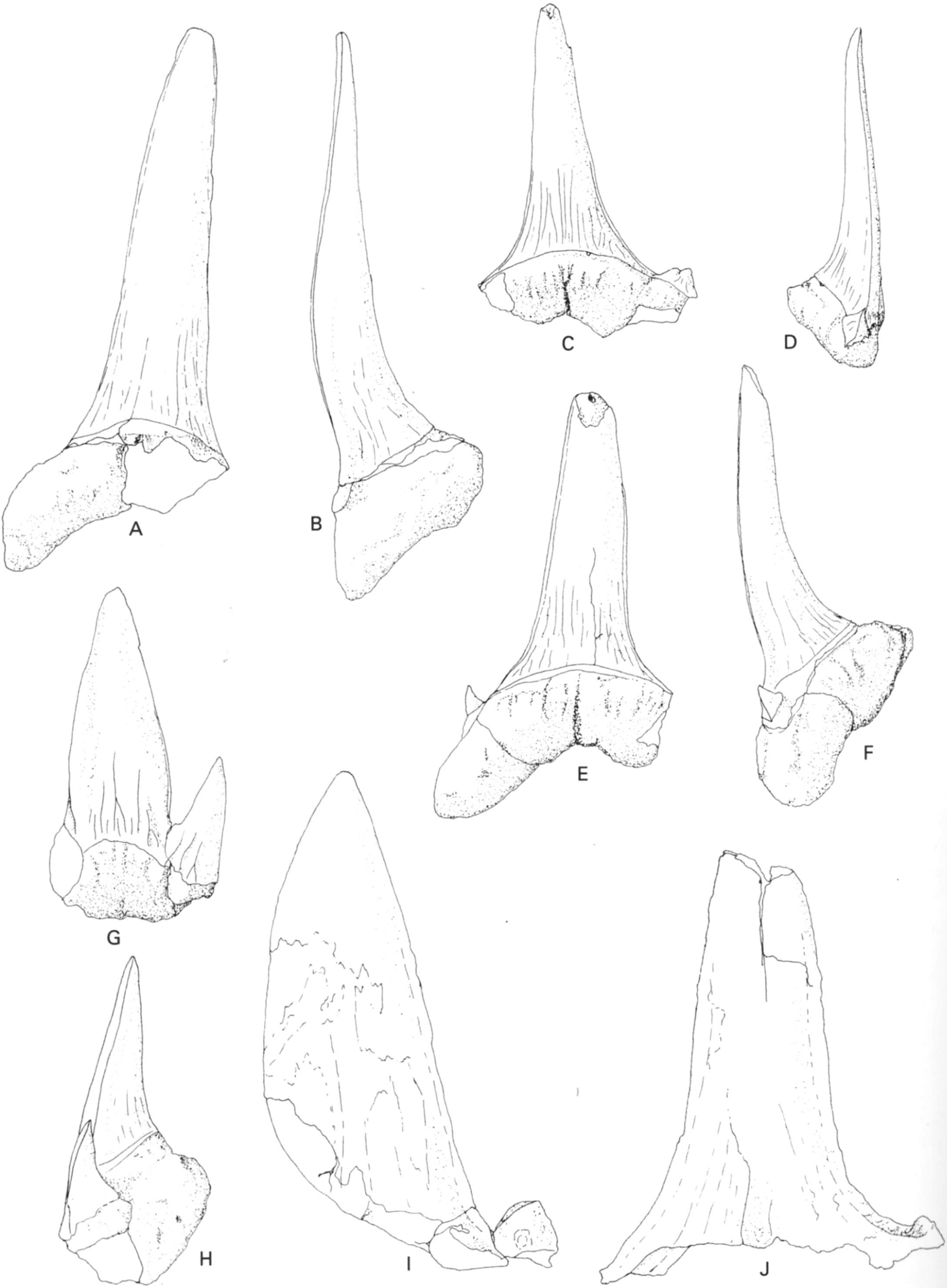

UPPER ALBIAN
LOWER CENOMANIAN
MIDDLE CEN.
auritus SZ
dispar Zone
mantelli Zone
inerme Z
rhot.Z.
Dulcey Dock Member
Weather Castle Member
Red Cliff Hole Member
Crowe's Shoot Member
I no. Bed 1
Totternhoe Stone Facies
DD1 DD2 DD3 DD4 DD5 DD6 DD7 DD8 DD9 DD10 DD11 DD12 DD13 DD14 DD15 DD16 DD17 DD18 DD19 DD20 DD21 DD22
WC1 WC2 WC3 WC4 WC5 WC6 WC7
RCH1 RCH2 RCH3 RCH4 RCH5
SLC 1 SLC 2 SLC 3 SLC 10 SLC 11 SLC 12
16 metres of Ferriby Formation not shown
SAMPLE POINTS
Synechodus dubrisiensis
Synechodus nitidus
Paraorthacodus recurvus
Notorhynchus aptiensis
Hexanchus sp.
Squalus sp.
Protosqualus sigei
Squalidae gen. indet.
Eoetmopterus ? sp.
Echinorhinid ? indet.
Squatina cf. cranei
Squatina sp.
Heterodontus canaliculatus ?
Chiloscyllium cf. greeni
cf. Hemiscyllium sp.
Pseudospinax heterodon sp. nov.
Pararhincodon cf. lehmani
Anomotodon principalis
Scapanorhynchus praerhaphiodon ?
Pseudisurus sp.
Cretoxyrhina mantelli
Leptostyrax sp.
Scyliorhinid ? gen. indet.
'Scyliorhinus' dubius
Cretascyliorhinus destombesi
Pteroscyllium ornatum sp. nov.
Galaeomorph gen. indet.
Squatirhina thiesi
Squatirhina ? sp.
Sclerorhynchoide gen. et sp. indet.



JUR.
L. ALBIAN
M. ALBIAN
UPPER ALBIAN
L. CENOM
?
dentatus Z.
cris.
orbignyi SZ.
var. SZ
auritus SZ.
dispar Zone
mantelli Z.
Kim. Clay
Carstone
Hunstanton Formation
Ferriby Fm.
1
2a
2b
2c
3
3/4
4
5A
5B
5C
6a
6b
7
8
9
10
11
1
2
0
1m
2m
3m
4m
SAMPLE POINTS
Synechodus dubrisiensis
Synechodus nitidus
Notorhynchus aptiensis
Protosqualus sigei
Protosqualus pachyrhiza sp. nov.
Echinorhinid ? indet.
Squatina cf. cranei
Squatina sp.
Heterodontus canaliculatus ?
cf. Hemiscyllium sp.
Pseudospinax heterodon sp. nov.
Cretorectolobus gracilis sp. nov.
Pararhincodon cf. lehmani
cf. Protolamna sp.
Protoscyliorhinus ? sp.
Cretascyliorhinus destombesi
Parasymbolus reticularis sp. nov.
Pteroscyllium ornatum sp. nov.
Squatirhina thiesi



2
1
0
Crown Height (mm)
Crown Height
Crown Width
Anterior and lateral teeth,
Gault Formation,
Folkestone
Posterior tooth, South Ferriby
Posterior tooth,
Folkestone
Anterior and lateral teeth,
Hunstanton Formation, Speeton
and South Ferriby
0
1
2
3
4
Crown Width (mm)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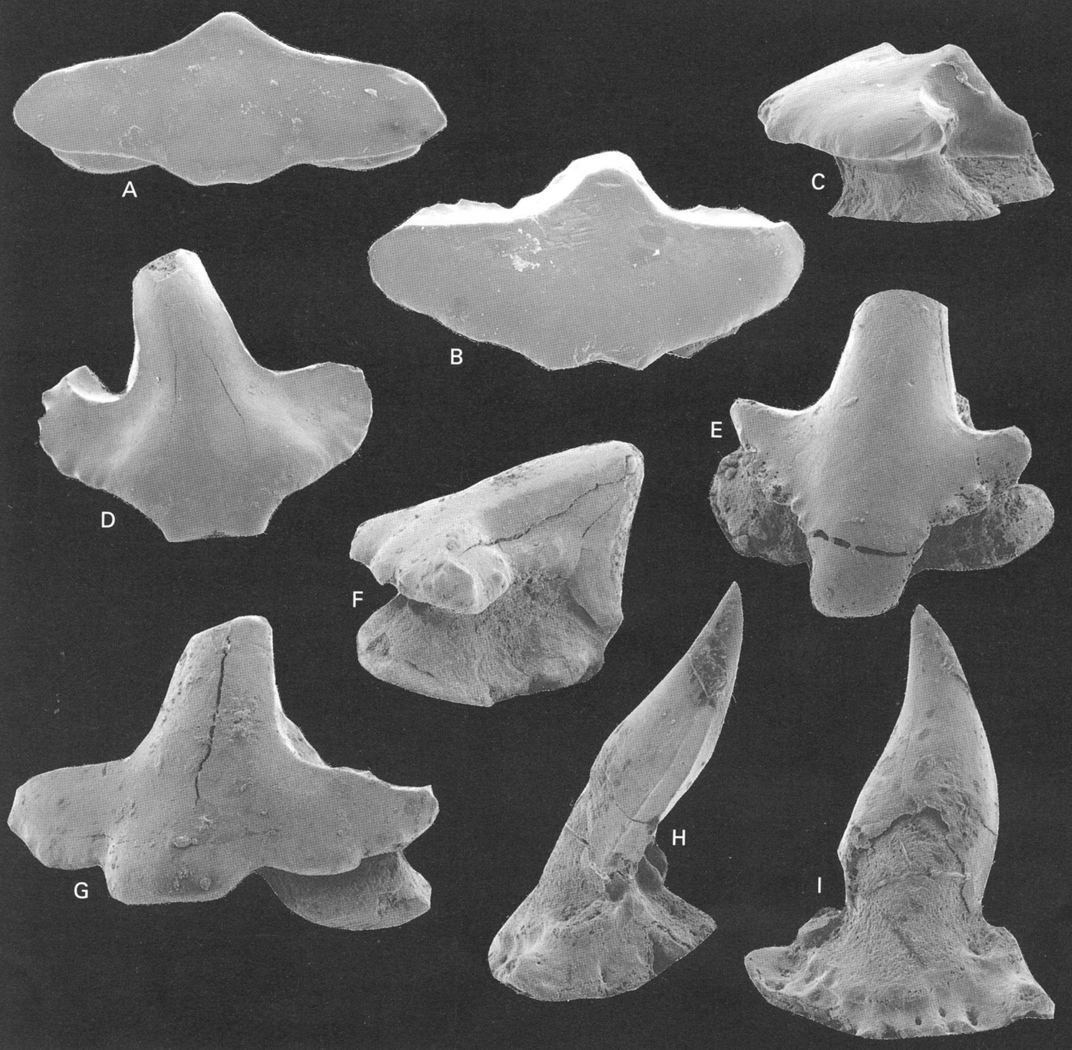
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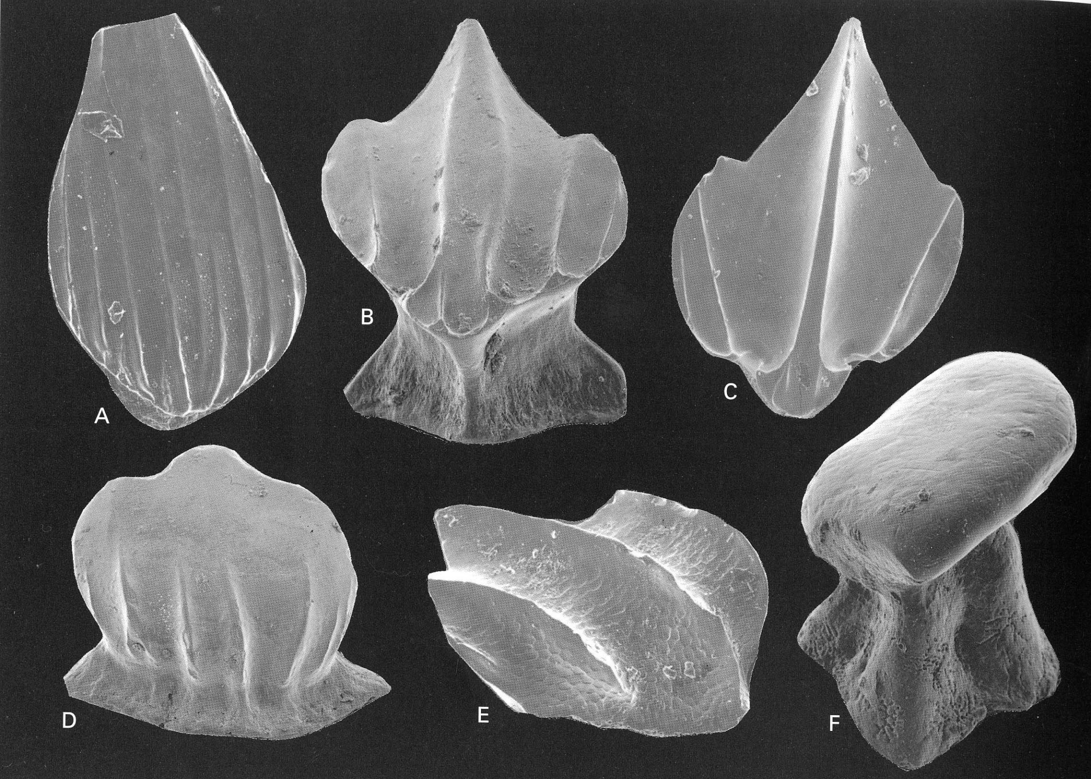
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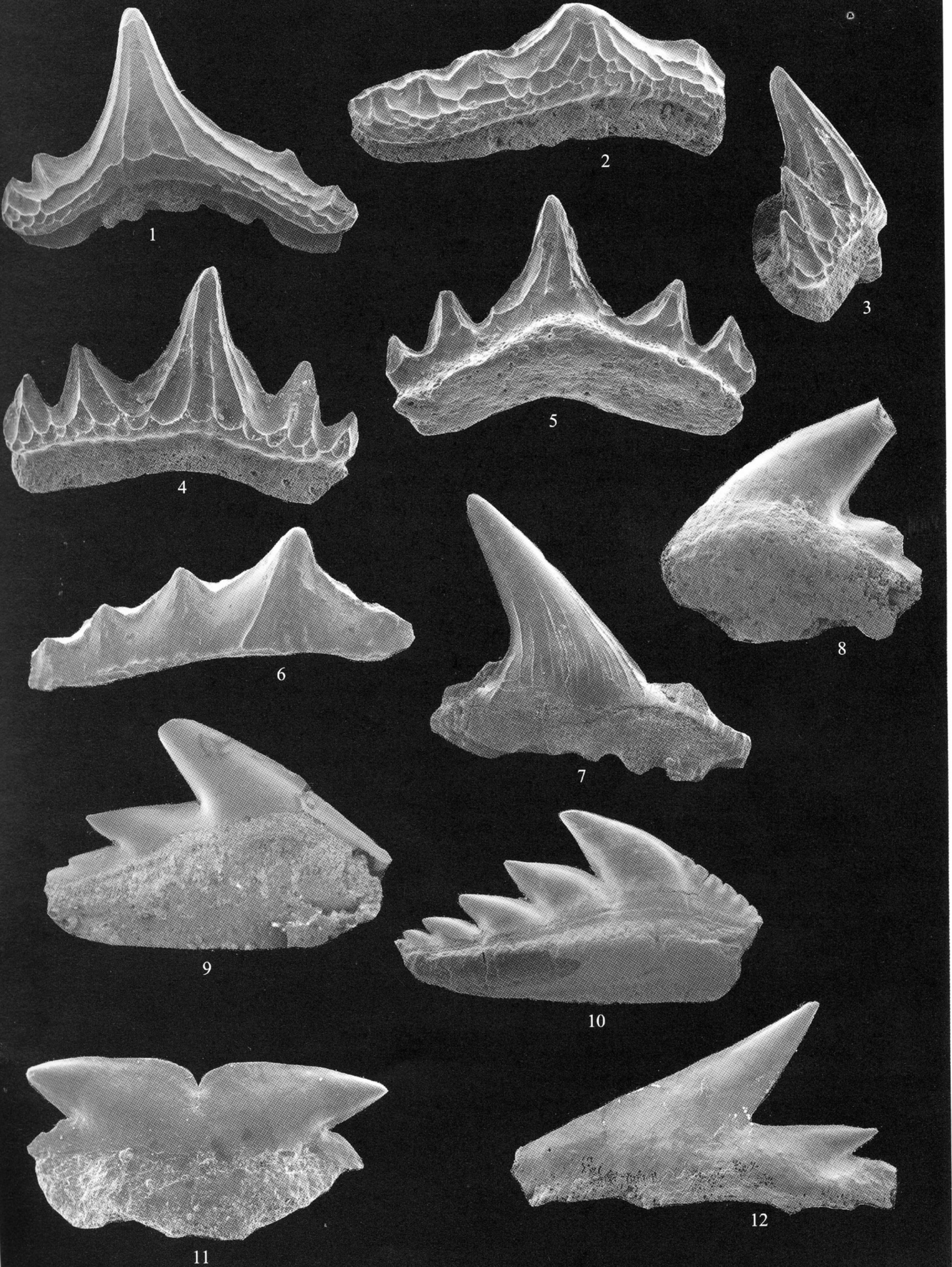
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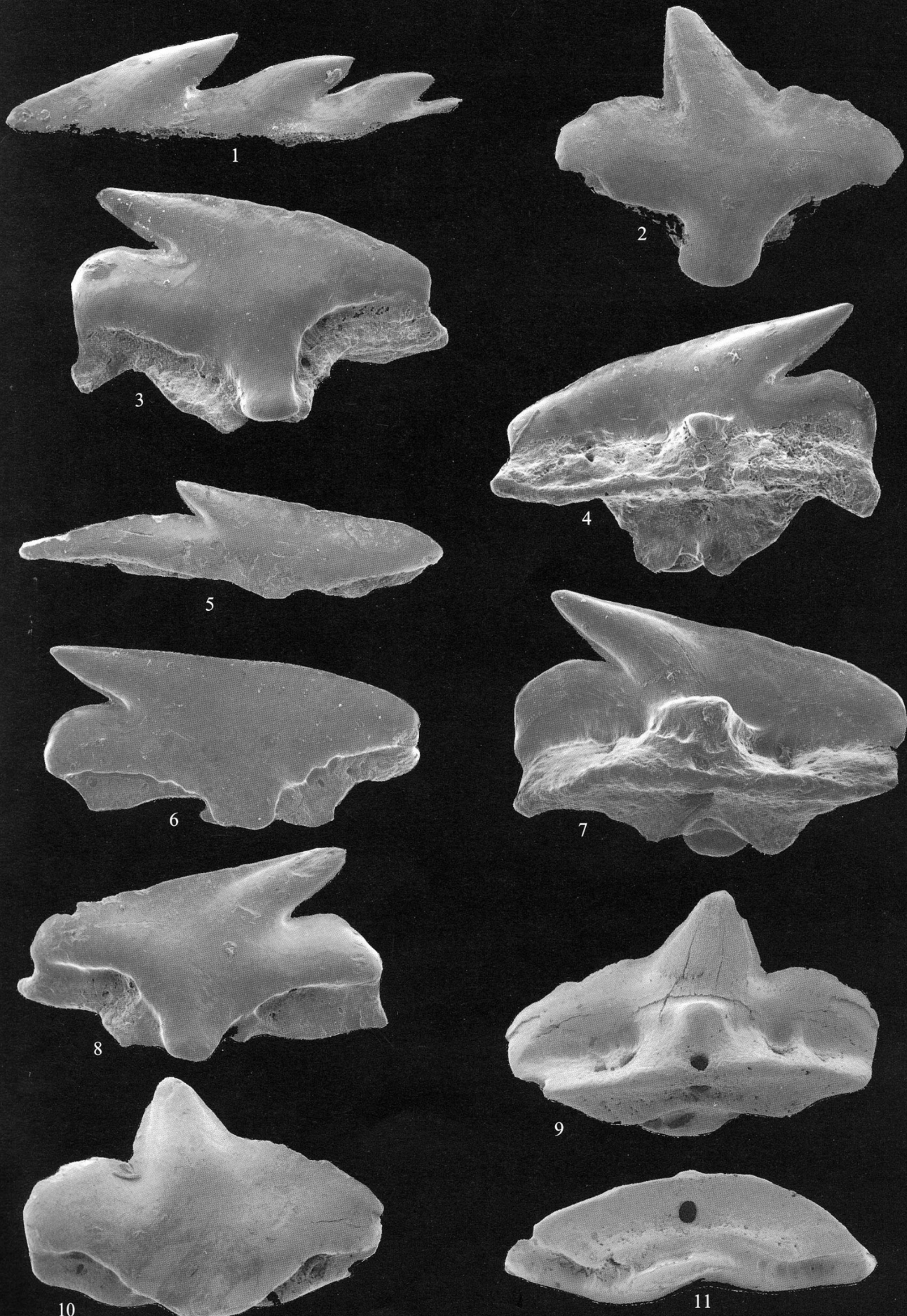
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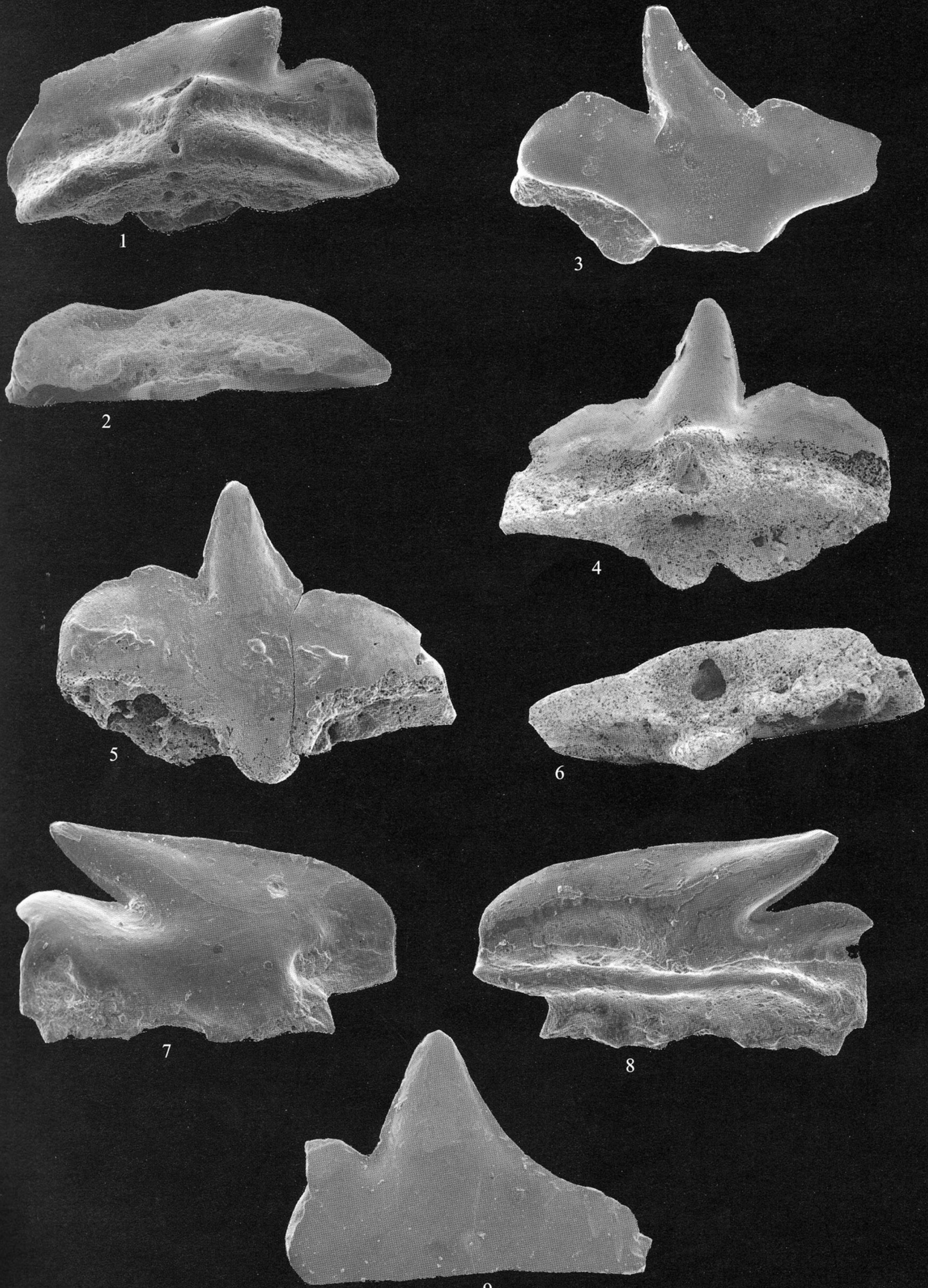
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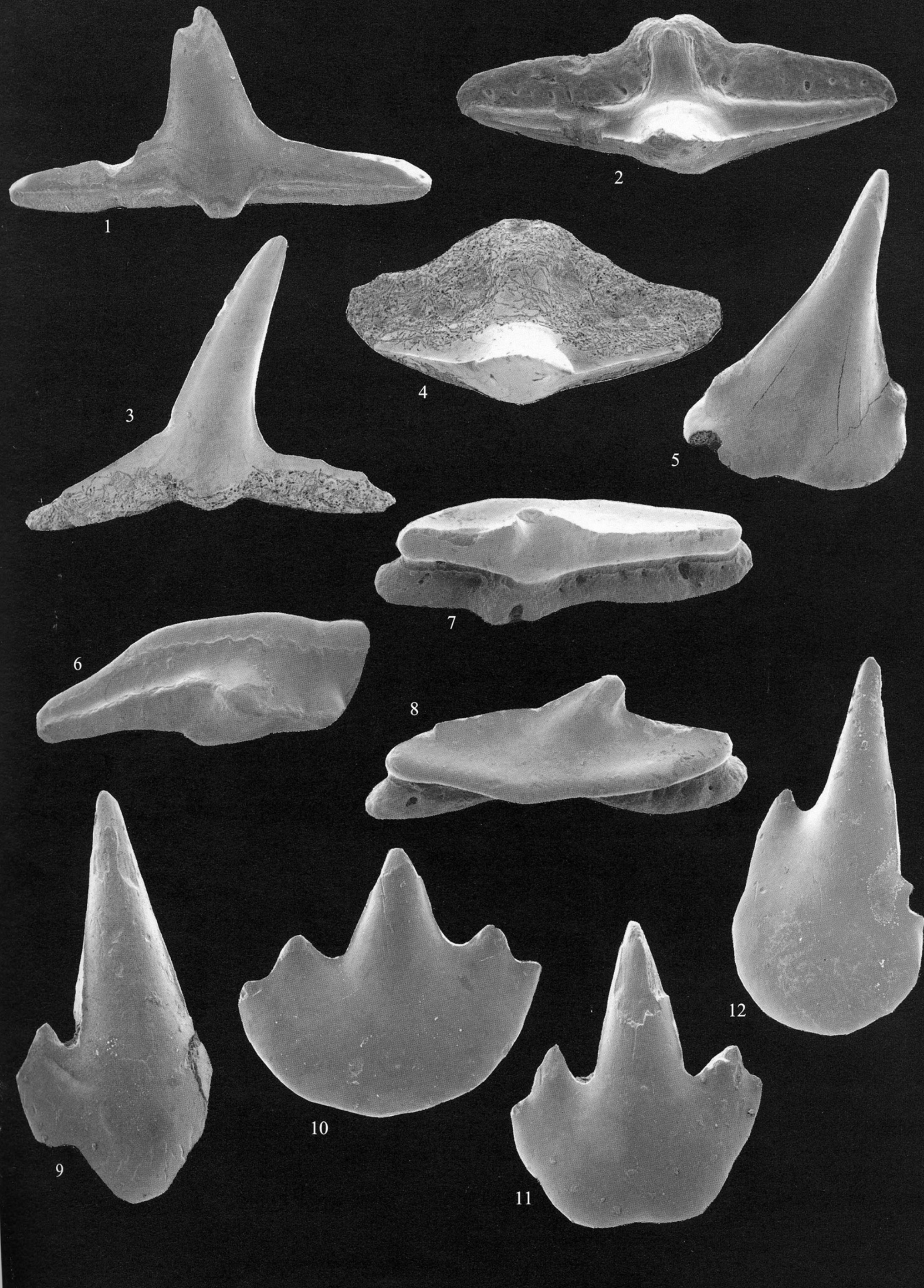
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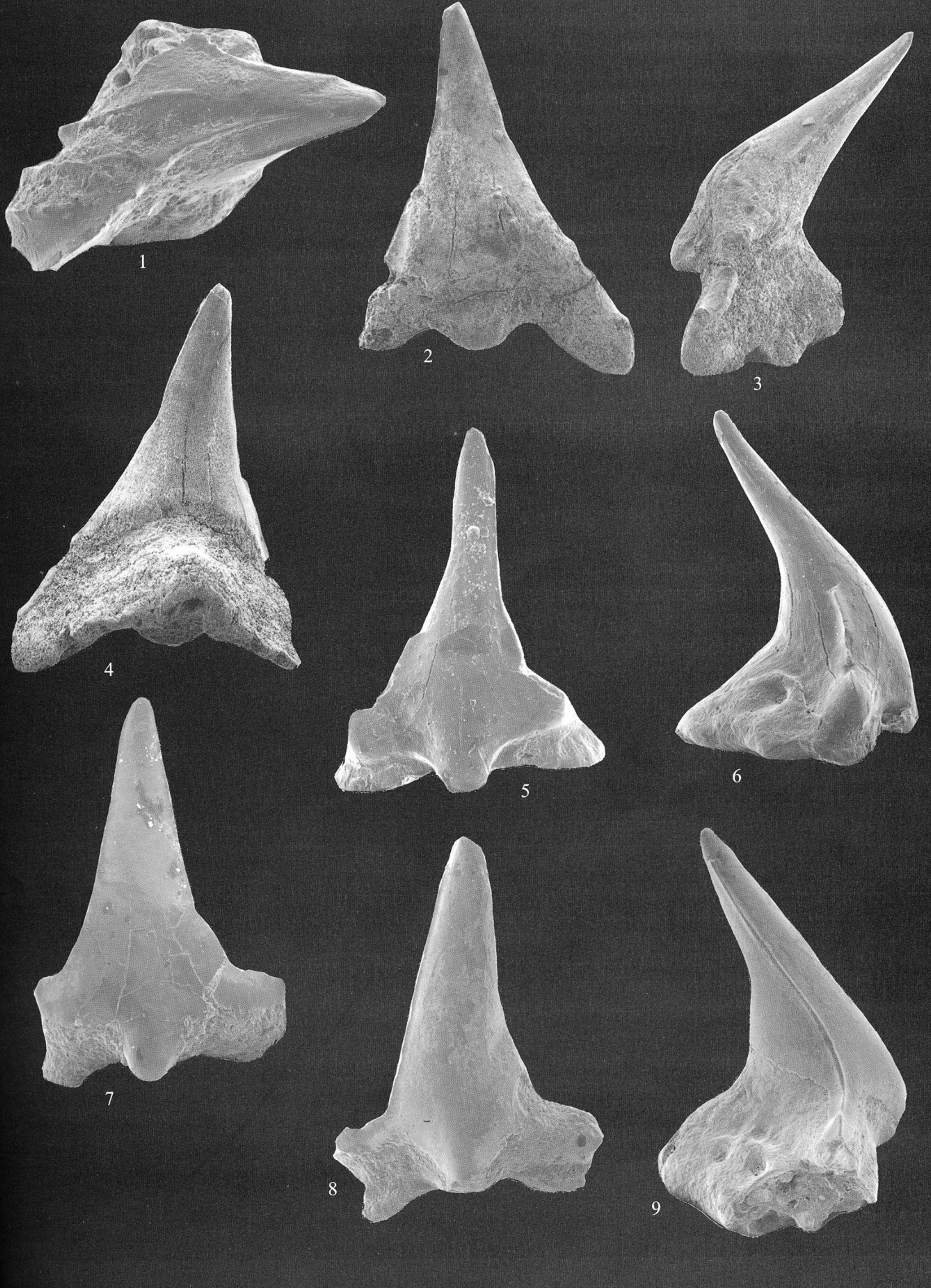
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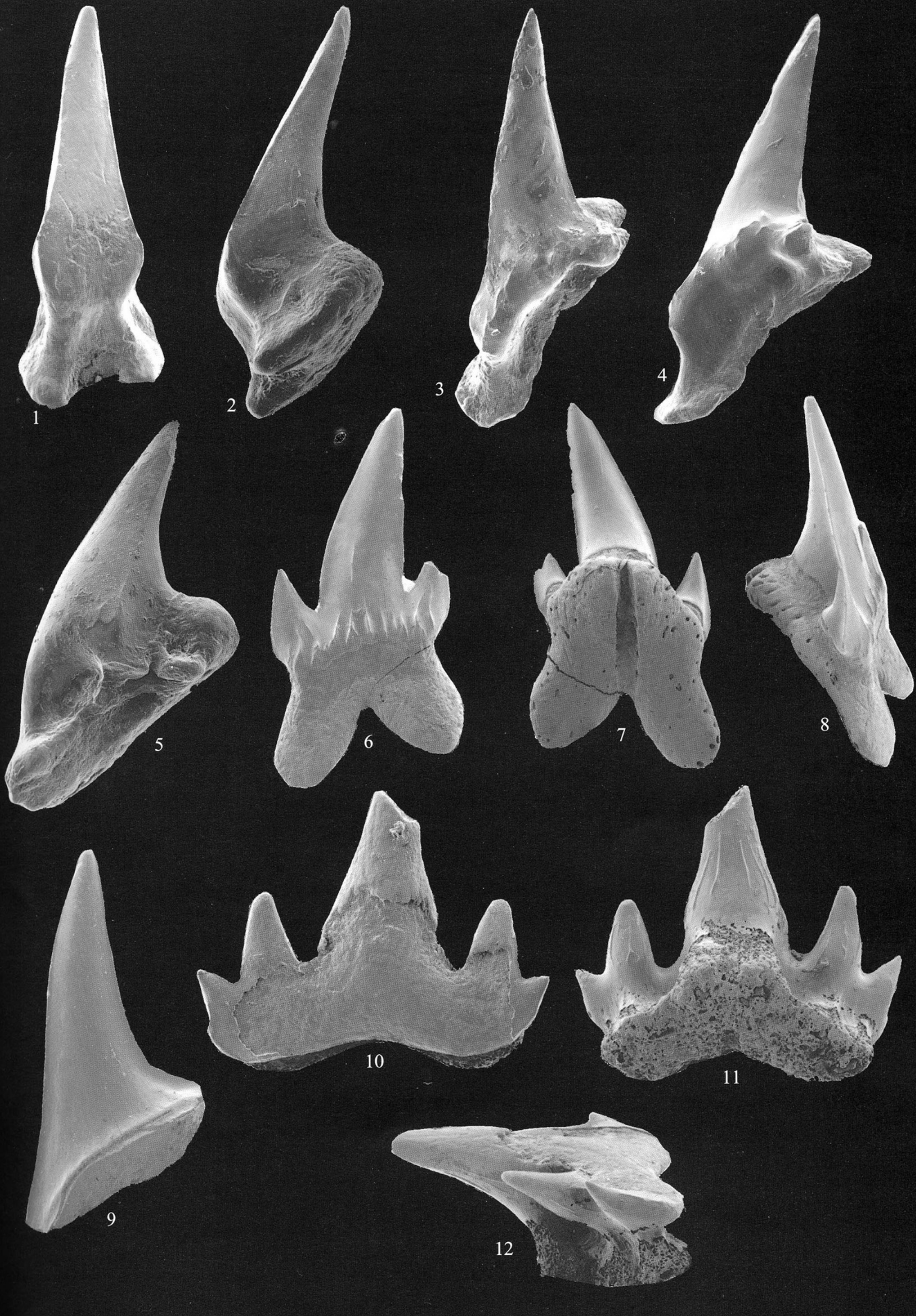
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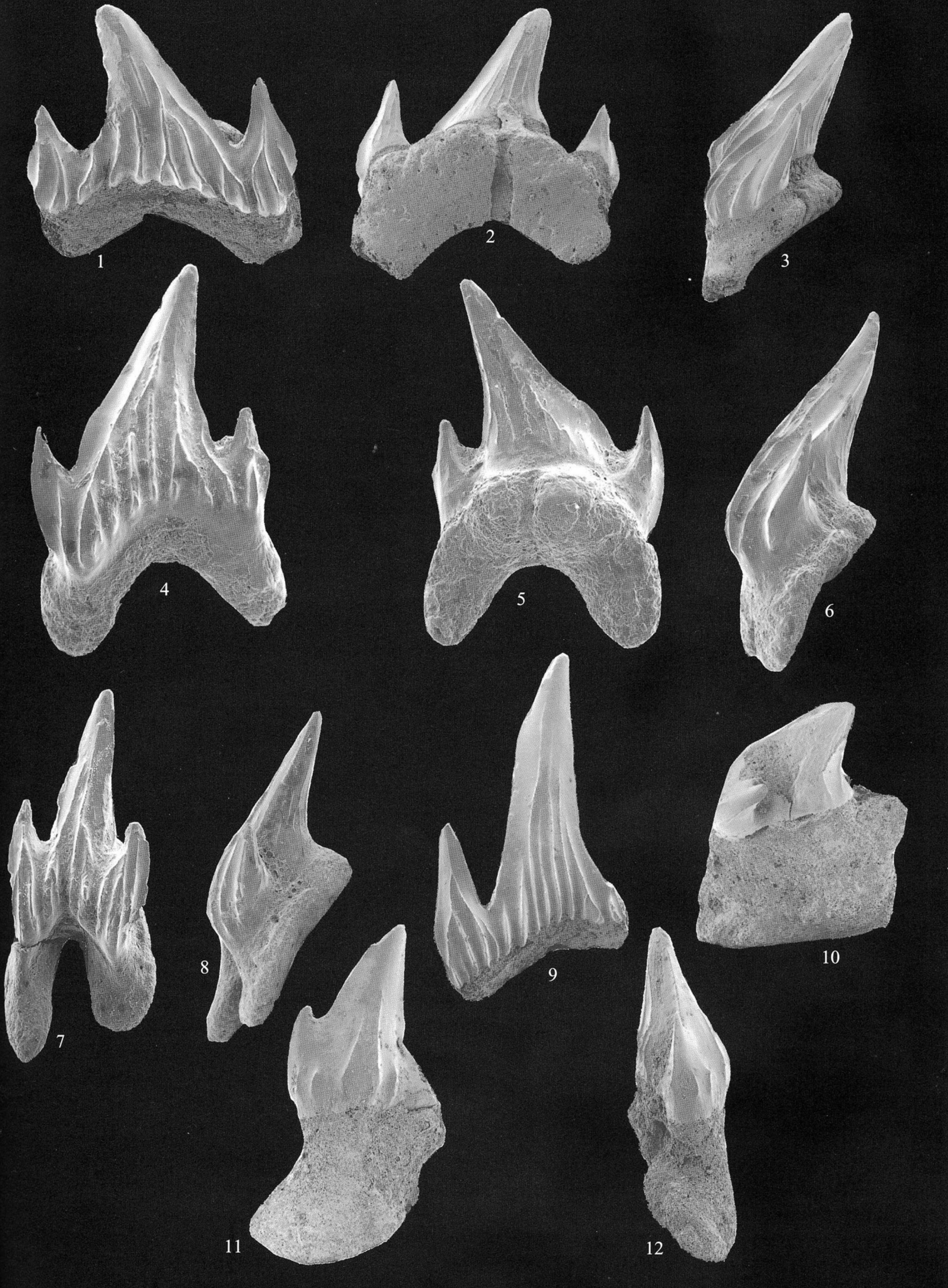
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